FORAGING STRATEGIES OF ADÉLIE PENGUINS AT BÉCHERVAISE ISLAND.

By

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DECLARATION

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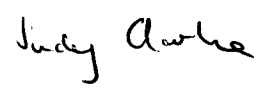

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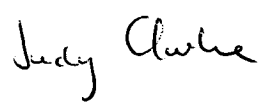

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ABSTRACT

A detailed multi-year analysis of the breeding biology, diet and foraging strategies of Adélie penguins (*Pygoscelis adeliae*) from the Béchervaise Island colony in East Antarctica was carried out in relation to gender and environmental conditions such as sea ice extent. Data on breeding success and foraging activities (location, trip duration, and diving behaviour) were collected during the 1994-95, 1995-96 and 1996-97 austral summers along with dietary samples. Analyses included data and samples from four previous seasons in addition to the new material.

Several hundred penguins of known sex within the colony were individually identified by means of implanted electronic tags to allow automated detection of their travel to and from their nest sites. Multi-year data on the nest and mate fidelity and breeding success of these birds were available for analysis. The breeding success and variations in foraging strategies (trip duration, diet, dive depth, and foraging location) of tagged individuals were analysed in detail over a number of seasons to study the ways in which these variables change from year to year and to determine how the variations relate to environmental factors.

Subcutaneously implanted transponders have proved to be a reliable means of identifying individual penguins, and the usefulness of these passive electronic tags was evaluated as the research project progressed. Survival of Adélie penguins carrying transponders over seven seasons was found to be equal to or better than that of birds with flipper bands, although not statistically significant on an annual basis. Survivorship of fledglings tagged as chicks was greater than that determined by previous researchers using banded populations of fledglings.

Occasional problems associated with the use of implanted transponders were observed. The transponder removed from one bird had developed a slimy biofilm harbouring potentially pathogenic organisms incorporated at the time of implantation. If such contamination was to be common the long-term survival of groups of birds carrying

implanted transponders could be lowered below that of unmarked populations. Migration of transponders away from the injection site into potentially hazardous locations, which might jeopardise survival in some individuals, was also demonstrated.

Such risk factors could limit the use of implanted identification devices in long-lived or endangered species. However, introduction of bacteria can be minimised by careful injection techniques and cleansing of instruments and skin with iodine or alcohol. The choice of a suitable implantation site, such as midway down the back, from which transponders may migrate without impinging upon vital structures, is also important. It was concluded that transponders, when used with care, provide a viable alternative to flipper bands in demographic studies of penguins.

Consistent sex differences in foraging trip duration, feeding locality and diet of breeding Adélie penguins were demonstrated at two widely separated locations over several breeding seasons. Differences in foraging behaviour were most pronounced during the guard stage of chick rearing. Female penguins made on average longer foraging trips than males, ranged greater distances more frequently and consumed larger quantities of krill (*Euphausia superba*). In contrast, males made shorter journeys to closer foraging grounds during the guard period and fed more extensively on fish throughout chick rearing.

Mean guard stage foraging trip durations over four seasons at Béchervaise Island, East Antarctica and over two seasons at Edmonson Point, Ross Sea ranged between 31-73 hr for females and 25-36 hr for males. Ninety percent of males tracked from Béchervaise Island by satellite during the first three weeks post-hatch foraged within 20 km of the colony, while the majority (60%) of females travelled to the edge of the continental shelf 80--120 km from the colony to feed during this period.

The overall composition of the Adélie penguin diet varied between seasons at both locations. However, krill comprised a greater proportion of the diet of female penguins than that of male birds at each colony during the guard period. Males on the other hand

tended to eat greater amounts of fish and amphipods than did females. These sex differences, although consistent from year to year, were however not statistically significant.

Analyses of the body masses of males and females departing on foraging trips of long and short duration (> and < 40 hr respectively) showed that the departure weights of birds prior to long trips were significantly lighter than were those prior to short trips. Birds, particularly males, were heavier at the start of the guard stage than at the end, and both sexes gained weight slightly over the crèche period.

The observed gender differences in trip duration, foraging location and diet are discussed in terms of energy requirements, intraspecific partitioning of foraging and territorial behaviour. The existence of a two-fold foraging strategy due to a trade-off between the allocation of food to chicks and the storage of parental body reserves is postulated. The relevance of such a foraging strategy to the breeding success of penguins in the Mawson region is discussed in relation to krill, fish and zooplankton distribution in the area.

Variations in the diving patterns of 18 Adélie penguins rearing chicks were examined over two breeding seasons in relation to foraging trip duration, gender and change in fast ice extent. Mean dive depth, duration and percent bottom time overall were 18.5 m, 1.02 min and 26.4% respectively. Maximal depths reached on individual trips ranged from 14 to 112 m. Twenty-seven percent of all dives were to depths <5 m; 54% were <10 m; 68% <20 m and only 11% >50 m. No diurnal patterns of diving frequency or depth were apparent.

Penguins making short trips (<40 hr) rarely dived deeper than 50 m, with 91% of all dives <40 m in depth. Most short trips took place during the guard stage when fast ice was present around the island. Long trips (>40 hr) occurred during both the guard and crèche stages, and showed a bimodal pattern of dive depths with the secondary peak occurring at 40-70 m. Mean dive depth, duration and percent bottom time all increased

as the ice extent reduced. The birds, particularly males, showed a tendency to make shorter trips and perform shorter, shallower dives when fast ice was present than when there was open water.

Male birds undertaking short trips showed significantly greater variability in mean dive depths and durations than did females on short trips or birds of either sex on long trips. Penguins of both sexes making long trips spent on average approximately fifty percent more time on the bottom than did those making short trips. Logistic regression analysis identified percentage of time on the bottom as the strongest indicator for discrimination between trips of long and short duration. No predictor variables were identified that could be used to discriminate between the trips of males and females.

The extensive foraging range of Adélie penguins in the Mawson region enables birds to forage in three distinct oceanographic zones each dominated by different micronekton communities. Most birds ingested larger quantities of krill (*E. superba*) on long trips than short, while consumption of fish was more common on short trips. The relationship between diet composition and diving behaviour on trips of different duration is discussed. Changes in diving behaviour as environmental conditions alter may reflect the capacity of penguins to modify their foraging strategies in response to spatial and temporal variations in the distribution of their prey.

The results of the studies described in this thesis provide some new insights into the foraging ecology of Adélie penguins in the Mawson region of East Antarctica. These may help facilitate the modification and improvement of existing ecosystem-based monitoring programs such as the Convention for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP), and also aid the interpretation of data from such programs.

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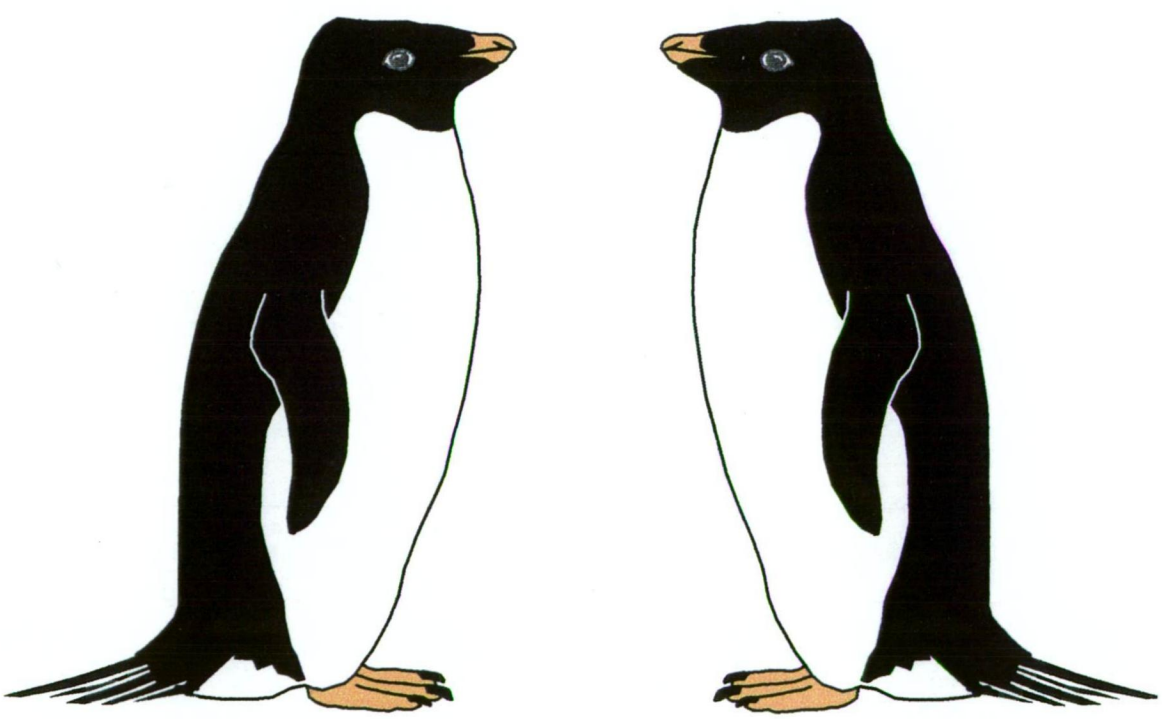

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CHAPTER 1: INTRODUCTION

1.1 ADÉLIE PENGUIN FORAGING ECOLOGY AND BREEDING SUCCESS

Adélie penguins are widely distributed around the Antarctic continent, breeding on rocky outcrops at latitudes between 56°20' and 77°35' South (Woehler 1993). They spend each winter at sea foraging within the pack ice zone and return to their breeding colonies during September and October to mate, incubate their eggs and rear their offspring through the summer months. Chicks fledge during late February and March during which time adult birds carry out their moult before departing to sea for the winter months.

During winter Adélie penguins are dispersed more widely than in summer, unrestricted by any ties with land, and have been shown to travel thousands of kilometres from their breeding colonies (Kerry *et al.* 1995a; Davis 1996; Lawless and Clarke, unpublished data). They remain closely associated with the pack ice (Ainley *et al.* 1992; Fraser *et al.* 1992), apparently drifting with it (Lawless and Clarke, unpublished data) and presumably resting on it when they are not foraging. Birds breeding in the Mawson region show a tendency to forage along the edges of the continental shelf at this time of year (Kerry *et al.* 1995a).

In contrast to the rest of the year, the foraging range of breeding Adélie penguins is restricted in summer by the need for the birds to return regularly to their nests to carry out incubation duties and then to feed their offspring. Adult birds travel up to 350 km from their colonies to feed during their multi-day trips in the incubation period (Davis and Miller 1992; Kerry *et al.* 1995a). Once the chicks have hatched, foraging trips are further limited by requirements for the provision of regular meals for the growing young. Thus Adélie penguins are closely tied to their breeding grounds throughout chick rearing and must find sufficient food for themselves and their offspring within a radius of approximately 120 km of their colonies during this period (Kerry *et al.* 1995a&b).

High levels of breeding success are dependent on abundant food resources during the breeding season. When prey are apparently scarce penguins tend to forage further afield and take longer to complete each foraging trip (Kerry *et al.* 1995b). They will forage to meet their own energy requirements but their chicks will die of starvation if food supplies are not sufficient to enable the adults to return to the colony at regular intervals. Chick growth is slowed and breeding success reduced if foraging trips during the guard stage become much longer than two and a half days (Kerry *et al.* 1995b; Ainley *et al.* 1998).

Foraging behaviour during the breeding season is likely therefore to be strongly influenced by food availability. Inter- and intra-annual variations in foraging trip durations, feeding locations and diving behaviour most probably reflect the birds' responses to food distribution and abundance. Study of these parameters may enhance our understanding of the factors that affect breeding success in these marine species. Differences in foraging behaviour between locations around Antarctica also provide insights into the variety of ways penguins interact with their environment during their reproductive cycle.

Foraging ranges of Adélie penguins vary between locations around Antarctica, as do environmental conditions and diet. Penguins breeding on the Antarctic Peninsula travel relatively short distances (14-60 km) to forage during chick rearing (Lishman 1985a; Trivelpiece *et al.* 1987; Wilson *et al.* 1989b, 1994), while those breeding on the continent tend to travel further (up to 120 km) and forage over the continental shelf as well as in deep water (Ridoux and Offredo 1989; Kerry *et al.* 1994; Ainley *et al.* 1998). Penguins in some regions feed under fast ice throughout the entire breeding season (Watanuki *et al.* 1993, 1994), while others forage in regions of seasonal ice cover (eg: Kerry *et al.* 1995a; Watanuki *et al.* 1997). Diving behaviour varies in relation to ice extent and diet, and pygoscelid penguins have been shown to exploit a wide range of depth strata depending on the nature of their environment and the prey species upon which they are feeding (Croxall *et al.* 1988; Whitehead 1989; Williams *et al.* 1992a;

Croll 1993; Watanuki *et al.* 1997). Adélie penguins breeding on the Antarctic Peninsula feed mainly on krill, while those breeding on the continent and foraging over the shelf bring back a wider range of organisms including fish, krill, amphipods and squid (Emison 1968; Puddicombe and Johnstone 1988; Kerry *et al.* 1994; Ainley *et al.* 1998).

The foraging behaviour of Adélie penguins has been a topic of interest among seabird ecologists over the past three decades, with studies occurring at a number of different locations under different environmental conditions. Research topics have included diet (eg: Emison 1968; Lishman 1985a; Coria *et al.* 1995), foraging locations (eg: Sadlier and Lay 1990; Davis and Miller 1992), energetics (eg: Culik and Wilson 1991a&b, 1992; Chappell *et al.* 1993b&c) and diving behaviour (eg: Naito *et al.* 1990; Chappell *et al.* 1993a). More recently there has been an emphasis on the interactions of these themes with each other and the environment, and a realisation that Adélie penguin foraging behaviour varies widely between locations and also between seasons. For example, it has been shown that Adélie penguins at Davis in Prydz Bay vary their dive depth depending on the major prey species captured (Whitehead 1989); those in the Ross Sea appear to forage more successfully when there is pack ice within their foraging range (Ainley *et al.* 1998); diving behaviour differs greatly between penguins foraging under the fast ice compared to those foraging in open water (Watanuki *et al.* 1997); and diet can vary both between and within seasons, reflected in foraging duration and diving behaviour (Watanuki *et al.* 1993; Ainley *et al.* 1998).

Breeding success is inevitably linked to foraging behaviour since food availability during the breeding season, especially in the guard stage (Boersma and Stokes 1995; Kerry *et al.* 1995b), determines the survival of penguin chicks to fledging. There has not been a great deal of research so far directed specifically at the relationships between the various aspects of foraging behaviour and breeding success. It is, however, known that foraging trip durations during chick rearing increase in seasons of low breeding success (Watanuki *et al.* 1993; Kerry *et al.* 1995b; Ainley *et al.* 1998), and that poor breeding seasons are often associated with years when fast ice persists longer than normal (Kerry *et al.* 1995b; Trivelpiece and Fraser 1996; Ainley *et al.* 1998). High

Adélie penguin breeding success on the Antarctic Peninsula tends to follow winters of extensive pack ice, and is assumed to be related to good spawning and juvenile survival conditions for krill (Fraser and Trivelpiece 1995).

1.2 BÉCHERVAISE ISLAND ADÉLIE PENGUIN MONITORING PROGRAMME

Study of the relationships between aspects of Adélie penguin foraging ecology and breeding success are important to further our understanding of Antarctic predator-prey relationships within an ecosystem context. Monitoring programmes are presently in place to determine the importance of krill in the diet of predator species such as Adélie penguins in order to better manage the future of krill fisheries in the Southern Ocean and to prevent over-exploitation of such resources.

An 1800 breeding-pair Adélie penguin colony at Béchervaise Island (67.58°S, 62.82°E) has been the site of such a long-term monitoring programme since the summer of 1990-91. This programme which utilises an automated weighing and recording system to log birds in and out of the colony (Kerry *et al.* 1993) is intended to continue indefinitely as part of the Convention for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP). The programme aims to monitor certain biological variables of selected species of penguins and seals with the objective of detecting changes in the marine ecosystem and attributing such changes to natural or man made (harvesting) causes.

The measurement of variables related to the breeding success and foraging efficiency of Adélie penguins at Béchervaise Island for CEMP forms the basis of a more detailed study of the long-term breeding biology and foraging ecology of these birds. This research includes dietary analysis throughout the chick rearing period combined with satellite tracking of birds over the whole breeding season to determine foraging locations and extent of foraging range. Time-depth recorders are used to obtain detailed dive data, and energetics studies using tritiated water undertaken to determine food and

energy intake of both chicks and adults. The automated weighbridge and identification system provides additional data on foraging trip durations and body mass changes to complement manual observations and dietary studies.

Prior to the commencement of this Masters project the monitoring programme at Béchervaise Island had begun to produce some interesting results. The timing of breeding and the foraging behaviour of penguins in the Mawson region were found to be quite different from those in other locations. Breeding events took place a week or more later than in most other regions (Ainley *et al.* 1983; Lishman 1985b; Whitehead *et al.* 1990; Kerry *et al.* 1993) and satellite tracking showed that the penguins commonly travelled long distances to feed compared with those on the Antarctic Peninsula (Lishman 1985a; Trivelpiece *et al.* 1987; Wilson *et al.* 1989b; Kerry *et al.* 1995a). Stomach content analysis showed that diet composition varied widely between and within seasons, providing additional evidence that Adélie penguins are not such obligate krill predators as had once been thought (Volkman *et al.* 1980; Lishman 1985a; Kerry *et al.* 1994; see also Emison 1968; Puddicombe and Johnstone 1988; Thomas and Green 1988; Ainley *et al.* 1998).

The foraging range of Adélie penguins along the coast of Mac.Robertson Land was shown to be at least 120 km (Kerry *et al.* 1992b, 1995a), enabling the birds to forage in three distinct oceanographic zones each dominated by different micronekton communities. These zones include the area over the continental shelf (neritic community), the continental slope zone (krill-dominated community) and the offshore oceanic zone (oceanic community) (Hosie and Cochran 1994). Data from satellite tracking and time depth recording, and analyses of foraging trip durations and stomach contents showed that birds foraged in both the krill-dominated and neritic zones, but predominantly in only one on any given foraging trip.

Studies of successive foraging trips in the 1992-94 breeding seasons (Kerry *et al.* 1994) showed that birds made a series of short trips of 15-18 km within the shelf zone, returning with amphipods, *Euphausia crystallorophias* or *Pleuragramma antarcticum*,

interspersed with longer journeys of 80-120 km to the shelf break from which birds returned with predominantly *E. superba*. The shorter trips tended to occur most when chicks were small and the longer trips once the chicks were left unguarded.

The masses of stomach contents of returning birds were less than 450 g when amphipods and fish were the major prey items and usually well in excess of this figure for birds returning with krill (Kerry *et al.* 1994). These results suggested that the foraging strategy of breeding penguins changes from making short trips of less than 30 hours and returning with amphipods and fish to making longer trips and returning with krill as the chick rearing period progresses.

The use of an Automated Penguin Monitoring System (APMS) to gather data was a new and innovative conception and allowed large amounts of data to be collected with minimal human interference (Kerry *et al.* 1993). Other methodologies such as the use of morphometrics and timing of incubation shifts were also developed in the early years of the programme (Kerry *et al.* 1992a; Clarke *et al.* 1995). In addition, cloacal sexing techniques were perfected and the effects of monitoring procedures on individuals and the colony as a whole examined (Clarke and Kerry 1994).

Results from several aspects of the programme had been published prior to the commencement of this thesis (Kerry *et al.* 1992a; Kerry *et al.* 1993; Clarke and Kerry 1994; Kerry *et al.* 1995a&b), but there were still a number of detailed analyses of both breeding biology and foraging strategies to be carried out. Differences in male and female foraging strategies had begun to emerge and it was also apparent that some of the inter-annual variation in foraging locations and diet could be related to sea ice extent and other environmental factors. Information on penguin diving behaviour had also been collected, and was available for analysis. An investigation of dive data in relation to diet, foraging location and sea ice extent was required in order to build up a more complete picture of how foraging Adélie penguins behave.

An understanding of the inter-relationships between the biological and environmental factors listed above is important in the context of a long-term monitoring programme to provide better insight into the causes of measurable variations (other than human harvesting of prey species) in the parameters being monitored. Thus the research described in this thesis was initiated.

1.3 Aims of this Study

The major aim of this study was to carry out a detailed multi-year analysis of the breeding biology, diving behaviour, diet and foraging strategies of Adélie penguins from the Béchervaise Island colony in relation to gender and environmental conditions, particularly sea ice extent. A secondary aim was to investigate some of the factors affecting breeding success and determine which parameters are most sensitive to variations in food availability.

Data on breeding success and foraging activities were collected during the 1994-95, 1995-96 and 1996-97 breeding seasons along with dietary samples. Analyses included data and samples from the previous four seasons in addition to new material. Many birds of known sex within the colony have been individually identified by means of implanted electronic tags to allow automated detection of their travel to and from their nest sites. The over-winter survival rates and variations in foraging strategies (trip duration, diet, depth, location) of tagged individuals were analysed in detail over a number of seasons to study the ways in which these variables change from year to year and to determine how the variations relate to environmental factors.

My thesis consists of six chapters including this introduction. Chapter 2 describes some of the general methods that are not covered in detail in Chapters 3-5. These include a detailed description of the study colony and the APMS, an overview of the stomach sampling and dietary analysis techniques used, and descriptions of various aspects of penguin handling and instrumentation.

Chapters 3-5 have been previously published (or submitted for publication) in journals and are presented minus their abstracts and with minor modifications appropriate to presentation in thesis format. Some additional data and discussion points have been incorporated into Chapters 3 and 4 on the basis of analyses subsequent to publication of the initial manuscripts. References have been incorporated into the reference list of the thesis as a whole. I was the primary author for all three papers; co-authors and journal details are provided as footnotes at the start of each chapter.

Chapter 3 describes transponder implantation techniques, and discusses potential problems with this technology as well as an analysis of colony demography over six seasons. Chapter 4 describes and analyses the gender variations in Adélie penguin foraging strategies that have been observed, including differences in foraging trip durations, foraging locations and dietary composition. Chapter 5 describes a study of Adélie penguin diving behaviour over two seasons in relation to stage of breeding, foraging trip duration and diet, and provides further insights into the gender differences in foraging behaviour described in the previous chapter.

The final chapter summarises the main findings of the project and recommends various factors for consideration in the further development of monitoring programmes, particularly the CCAMLR Ecosystem Monitoring Program (CEMP).

CHAPTER 2: GENERAL METHODS

2.1 STUDY SITE

The Adélie penguin colony on Béchervaise Island (67°35'S, 62°48'E) consists of approximately 1800 breeding pairs and is one of the smallest colonies in the Mawson region where more than 80,000 pairs of Adélie penguins breed annually along 40 km of coastline (Woehler *et al.* 1989). Béchervaise Island is located 2 km NW of the Australian Antarctic Station of Mawson, approximately 110 km from the edge of the continental shelf break (defined as the 1000m isobath as per Thomas and Green (1988)). During winter 30-40 km of fast ice is attached to the coast, and beyond this pack ice extends northwards to approximately 59°S (Jacka 1983, Zwally *et al.* 1983). The ice edge retreats progressively from October onwards, and open water is usually present to the coast in the Mawson region by late January.

Béchervaise Island was chosen as a monitoring site due to its topographical suitability for the installation of a weighbridge system (Fig 2.1). The colony is comprised of 18 semi-discrete sub-colonies, designated A - R (Fig 2.2). Sub-colonies K, L, M, N and Q, containing approximately 600 nests, were selected for servicing by the Automated Penguin Monitoring System (APMS) described in section 2.3. This study group was semi-isolated through the addition of short distances of 300 mm high wire netting fences to the natural rock boundaries. The remaining sub-colonies were set aside as minimum interference controls. Birds moving into the study area followed a well-defined path through a natural gateway. The weighing platform and associated detection systems were placed at this gateway (Fig 2.2).

Figure 2.1
Aerial view of the Béchervaise Island study colony prior to installation of the APMS. An arrow marks the site at which the weighbridge was subsequently located.

Three hundred nests within colonies K, L and Q were marked with numbered plastic tags nailed to the basement rock. At the commencement of the research programme the occupants of most of these nests were tagged with implanted electronic identification transponders (containing unique encoded 16 digit numbers), and their sexes determined by cloacal examination. Each subsequent year the nests were checked for tagged birds so that any untagged individuals present could be given transponders early in the breeding season. See Chapter 3 for further details on transponder implantation. By the end of the 1998-99 season 461 adult males and 466 adult females had received transponders. A proportion of birds were also flipper banded during the first four seasons of the programme; on the left flipper for males and on the right for females. Fledgling chicks were also tagged (but not banded) annually at a rate of up to 300 per

year. A total of 1684 fledglings from Béchervaise Island had received transponders by March 1999.

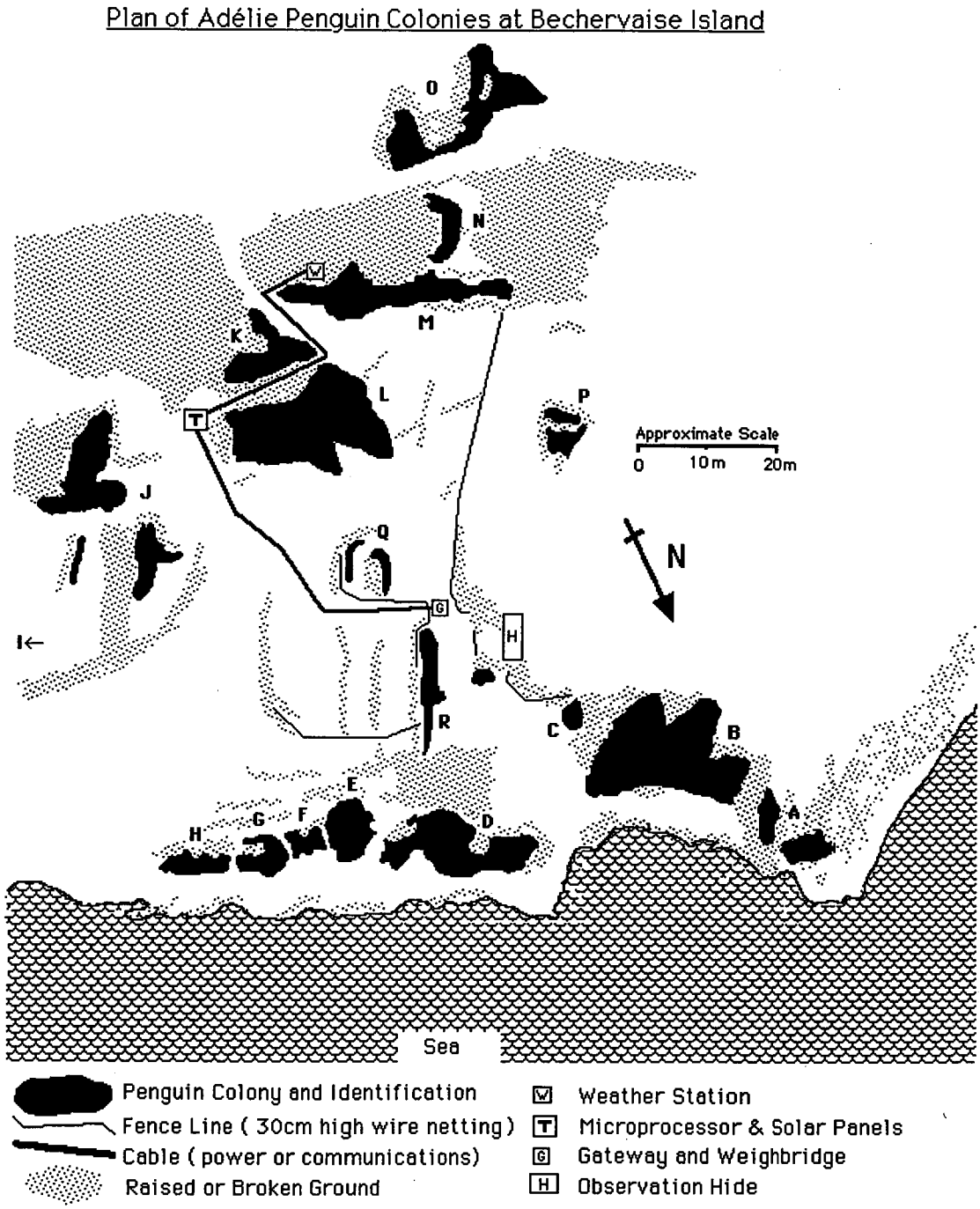


Figure 2.2
Location of the Automated Penguin Monitoring System (APMS) in relation to the layout of the Adélie penguin sub-colonies at Béchervaise Island (from Kerry *et al.* 1993).

Transponders were also implanted into 733 fledglings at Verner Island (5 km east of Béchervaise) between 1994 and 1999. The colony at Verner Island has been designated as an undisturbed monitoring site only visited once a year to tag fledglings. A second APMS has been installed at this site to allow comparisons with data from Béchervaise Island in future years. Adults and chicks have also been tagged and an APMS installed at Edmonson Point in the Ross Sea as part of a collaborative programme between Australia and Italy. Data from this location were used in the study described in Chapter 4.

The APMS at Béchervaise Island ran continuously throughout each breeding season since its installation in the summer of 1991-92. Movements of tagged birds to and from the colony were monitored by the system, which provides data on identity of bird, weight, time of day and direction of travel for each recorded crossing. All marked nests were also observed once or twice daily throughout each breeding season in order to cross-check and validate APMS records, and to enable gaps in the data to be identified.

2.2 Adélie Penguin Breeding Cycle (Mawson Coast)

After spending winter in the pack ice Adélie penguins arrive at their breeding colonies on land at the end of October. Males tend to arrive in the colony before the females, and the heaviest birds (usually established breeders of five years of age or more) appear first. The males usually occupy the same or nearby sites as in previous years, and females tend to search for their previous partner, especially if they have successfully reared chicks together in the past. Courtship and nest building last for 2-3 weeks after which egg laying commences.

Females usually lay two eggs in late November, the second being laid two days after the first. A third egg may be laid if the first egg is lost, and occasionally three eggs will be seen in a nest. Some birds may depart after only laying a single egg. Once she has laid her second egg the female usually departs immediately to sea to feed. She remains away

for 11-25 days (mean of 17) while the male incubates the eggs. On her return she takes over incubation duties and the male goes to sea to feed for 7-25 days (mean of 14). He returns shortly before the chicks are due to hatch (incubation lasts 33-35 days) and from then on the parents swap over every 1-5 days until the chicks move into crèches at approximately three weeks of age. For the next 4-5 weeks both parents forage simultaneously, returning to feed the chick(s) every few days. Some parents will raise two chicks to fledging, but most raise only one. A number of nests fail completely, the rate varying from year to year. At 7-9 weeks of age (late February) the chicks have replaced their down with adult feathers and are ready to go to sea.

Young Adélie penguins first return to their natal colony at 2-4 years of age and rarely breed on their first visit. These non-breeders usually appear in the colony at about the time that eggs start to hatch, and often cause disturbance to established nests as they try to find territories of their own. They stay around throughout the guard period after which their numbers lessen. Occasional juveniles (1-yr olds) appear in the colony to moult late in the season also. Females first breed at 3-4 years of age while males often wait until they are 4-5 years old (Ainley *et al.* 1983).

2.3 AUTOMATED PENGUIN MONITORING SYSTEM (APMS)

Weights and times of day of individual penguins moving in and out of the colony were recorded by an Automated Penguin Monitoring System (APMS) developed by the Australian Antarctic Division for the Adélie penguin research programme. The APMS consists of a weighbridge, an electronic tag reader, a direction sensor and a data-logging device (Fig. 2.3). It first became operational at Béchervaise Island in December 1991. Additional APMS units were installed at Verner Island (5 km from Béchervaise) in 1995-96 and Edmonson Point in the Ross Sea in 1994-95. At each site fences direct the penguins across the platform as they travel to and from the colony. Time, identity and weight data are logged as each one crosses.

a)

b)

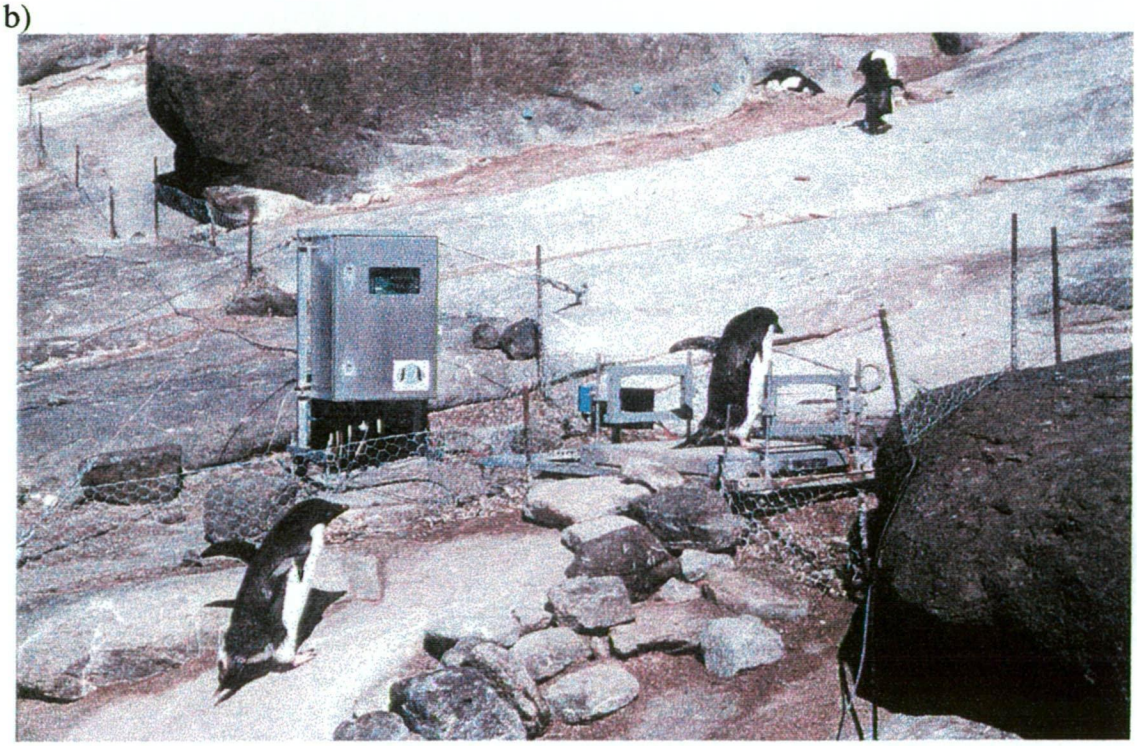


Figure 2.3
The Automated Penguin Monitoring System (APMS) in use at Béchervaise Island: a) close-up view of the weighing platform, tag detection antennae and direction sensing units; b) view including the box containing the microprocessor system. Power is provided by solar panels (out of sight).

The weighbridge is a low profile stainless steel platform (600 X 600 X 50 mm) which sends weight data to a microprocessor 20 times per second when a penguin is present. An algorithm is applied to the pattern of weights from each bird to determine the final figure to be sent to the data logger. A weight error is recorded on occasions when the bird crosses too quickly for a valid series of weights to be obtained, or when multiple birds step onto the platform together causing the weight to exceed a set threshold. The final weight is recorded to the nearest gram and the scales have an accuracy of better than ±5% of the static load. The weight of a bird crossing at walking pace is obtained in less than two seconds.

The direction of travel of a penguin across the weighbridge is sensed by a pair of infra-red beams according to the order in which the beams are cut whilst the bird is on the weighing platform. A directional error is recorded if the beams are cut in the wrong sequence such as when two birds are on the platform or a bird does not complete its crossing before turning around.

An electronic tag reader is incorporated into the APMS, with the antennae placed either side of the weighbridge. These can detect an implanted tag through the body of a penguin at a range of up to 0.7m. Individual tags, if present, are read as the bird crosses the weighbridge. A hand-held version of the tag reader also exists and is used to identify birds at their nests when necessary.

A microprocessor controls the various functions of the APMS and records inputs from the component parts. Each crossing of the weighbridge generates a data set comprised of a colony identification character, date, time and direction of travel, penguin weight and tag number, and error flags. Data are stored in the memory of the data logger and are downloaded regularly onto an IBM compatible computer for further analysis.

2.4 STOMACH SAMPLING

Stomach contents were collected from five breeding penguins every five days throughout the guard and crèche stages of chick rearing. The method used was based on the water-offloading method of Wilson (1984), and was carried out on birds captured on return from their foraging trips, prior to feeding their chicks. This method has now been incorporated into the CEMP Standard Methods (SC-CAMLR 1997), and is as follows:

A stomach pump or a funnel and tube (12-15 mm diameter) was used to introduce water into the stomach to dilute the contents and stimulate regurgitation. The tubing was made of soft latex and was tested at low temperatures to ensure that it remained flexible in cold conditions.

Stomach contents were collected by gently pumping up to 1000 ml of warm sea water via the stomach tube into the bird which was held standing, or lying in ventral recumbency. The stomach tube was inserted by opening the bill and gently feeding the tube down the throat to a distance equivalent to the base of the sternum (the tube was marked beforehand to this length). If resistance to intubation was encountered the tube was removed and tried again. A different individual was selected if resistance to the tube persisted.

Water was pumped gently into the bird. Pumping was stopped after 1000 ml had been introduced or once water started to dribble from the beak. Introduction of water was stopped sooner if the abdomen felt highly distended in birds that were very full of food. The tube was then removed and the bird inverted over a bucket. The abdomen was squeezed firmly while holding the beak open and massaging the back of the throat with a finger. Once the bird ceased to regurgitate it was returned to the starting position and the procedure repeated as many times as was necessary to remove all the stomach contents (i.e.: until the regurgitated water was clear and the stomach felt empty on palpation).

Extracted food samples were poured into a sieve to drain off the water and then preserved in absolute ethanol or frozen until sorting could take place. The birds from which samples had been taken were marked with dye prior to release so that they could later be observed at their nests to ensure that they were indeed breeding adults and to check that they had suffered no ill effects from the flushing procedure.

2.5 Dietary Analyses

Food samples were poured through a sieve to drain off the water and then preserved in plastic pots in absolute ethanol until sorting took place.

It proved to be difficult to drain samples of varying sizes, composition and state of digestion in a suitable way to obtain comparable wet weights. Two drainage methods were thus compared: a) where samples were compressed by a 1 kg weight for 2 minutes, and b) where all free water was gently pressed out through the sieve (1.0 mm mesh) without breaking down the food items more than they already were.

Both methods were used on the same samples and results showed that the wet weights obtained differed by an average of 30%, with those obtained using the first method almost always heavier than those from the second. There was, however, a wide range in the percentage mass difference (0-60%) between the two methods depending on the volume and consistency of each sample. Larger samples and those containing semi-digested matter retained more liquid than small or relatively undigested samples.

It was found that method b), where all obvious free liquid was removed without further breakdown of organisms, gave the most consistent and comparable wet weights; this method was thus used for all the dietary analyses described in this thesis.

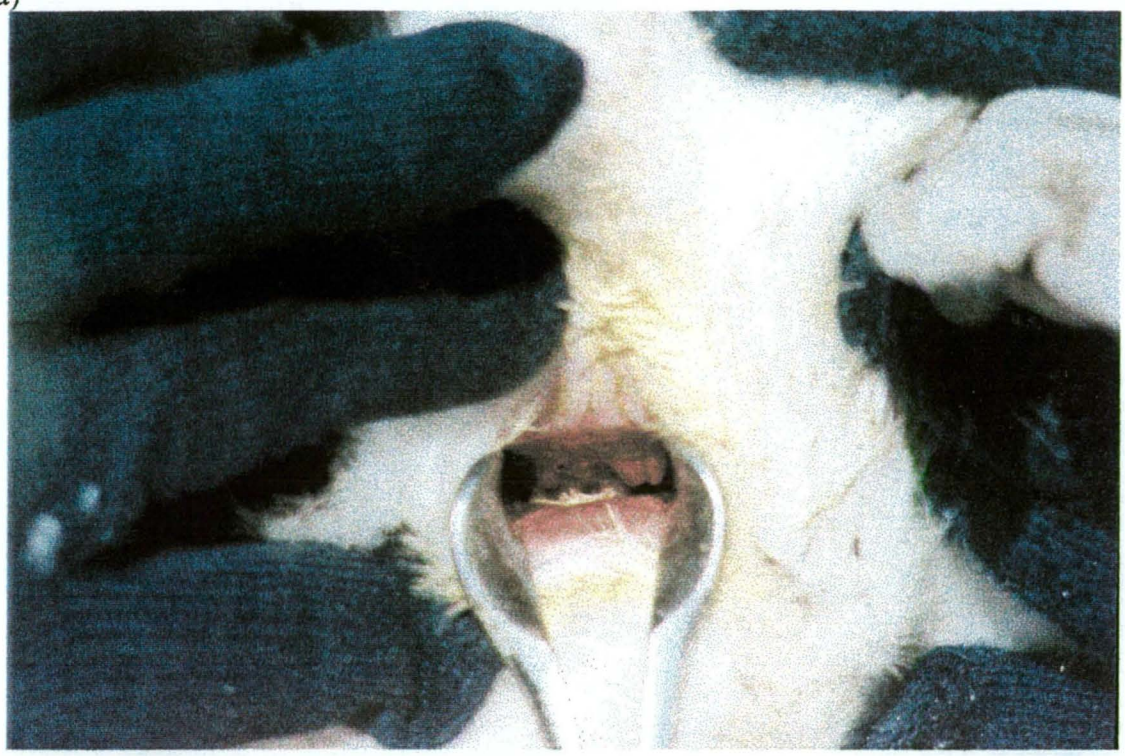
The fully drained sample was sorted into major components, and the weights of each recorded separately. Where the total sample was larger than 200-300g only a sub-sample (~150g) was sorted, and the component weights of the sub-sample multiplied up to the correct proportions of the whole. Samples were sorted into the categories of: *Euphausia superba, E. crystallorophias*, amphipods, fish, squid and krill mush. Wet weights of each of these categories were used for the dietary analyses described in Chapter 4.

2.6 Capture, Restraint and Sex Determination

Penguins used for transponder implantation and instrument attachment (see section 2.7) were captured at their nests while those from which stomach samples were collected were caught as they returned from the sea, prior to reaching their nests. Transponders were subcutaneously implanted into untagged adult birds from marked nests during the incubation period each season. Birds were removed gently from their eggs, which were kept warm and protected from skuas in an insulated container during the time the adult was being handled. The details of the tag implantation method are described in Chapter 3. Birds were restrained for the minimum time necessary to carry out sexing and tagging procedures and then returned to their nests by releasing them at the colony margin after replacing the eggs upon the nest. Birds for instrument attachment were captured during changes of guard duty while their mates were present at the nest. The mate thus took care of the chicks while the instrument was being attached to its partner. Procedures were again carried out as quickly as possible.

Birds from which stomach samples were to be taken were captured using a hand net as they returned to their nests from foraging. Each was weighed and sexed and then stomach flushed as described above. Released birds were observed for signs of ill effects until they returned to their nests minutes to hours later.

a)



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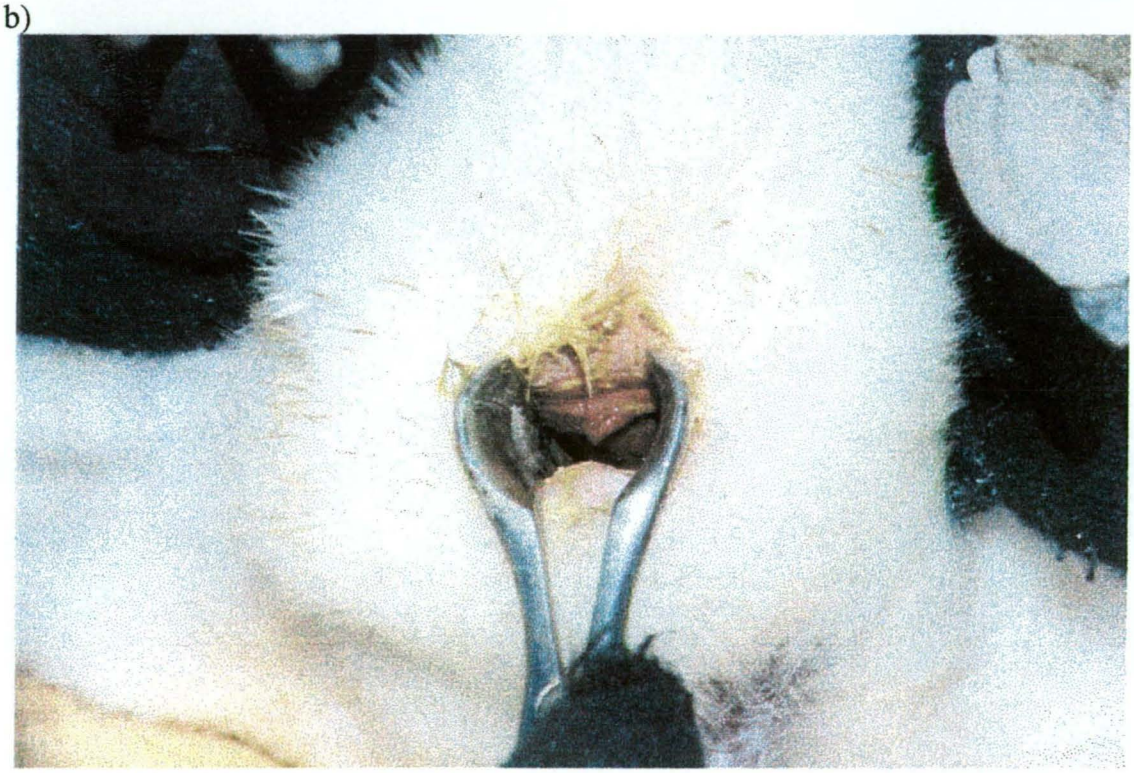


Figure 2.4
View of a) all four cloacal papillae of a male Adélie penguin and b) left urethral papilla and swollen tissue around the oviduct opening of a female. Both birds are in ventral recumbency.

Sex determination was done by cloacal examination as described by Sladen (1978). Each bird was held in ventral recumbency with its head tucked under the seated holder's arm, and its rear end on their knees aimed at the person carrying out the cloacal examination. The tail was held up out of the way while a speculum (human nasal type) was inserted. Faeces were gently wiped away until a view of the papillae hanging from the roof of the cloaca was obtained. It was sometimes necessary to move the speculum in and out a few times to dislodge a flap of mucosa that can trap the papillae out of view within the cloacal bursa.

Male breeding adults have four distinct papillae, two on each side (Fig. 2.4a). The medial pair are the urethral openings and the lateral two contain the termini of the vas deferens. Females have the pair of urethral papillae present but the genital pair are replaced by the oviduct opening on the left (Fig. 2.4b) and a small vestigial papilla on the right.

The oviduct opening was often difficult to visualise clearly and tended to be accompanied by bruising and oedema (especially post-lay). The papillae of male birds were most easy to recognise (four distinct firm papillae); females were sometimes identified on the basis of "absence of maleness".

2.7 INSTRUMENTATION

Platform terminal transmitters (PTTs) used for satellite tracking and time-depth recorders (TDRs) used for diving depth studies were glued using a fast-setting cyanoacrylic glue (Loctite 401™) to the centre of the lower back (Fig. 2.5). Instruments were positioned as far towards the rear of the bird as possible without inhibiting tail movement or obscuring the preen gland. The feathers were first cleaned with alcohol and dried. Glue was then worked well into the feathers to maximise bonding, and also applied to the sanded base of the instrument. The device was pressed down onto the

bird and held firmly in place until the glue set (one minute). Three cable ties were then tightened around each PTT, or one around each TDR. The cable ties were threaded between the feathers and the skin, with entry and exit points close to the edges of the device to prevent water penetration (Fig. 2.5).

Removal was achieved by first cutting the cable ties and then breaking the layer of glue so that the PTT could be peeled off. Feather damage was minimised on removal by using a blunt knife to break the glue layer and to lever the device off. Further details on instrument deployment, function and retrieval of data are described in Chapters 4 and 5.

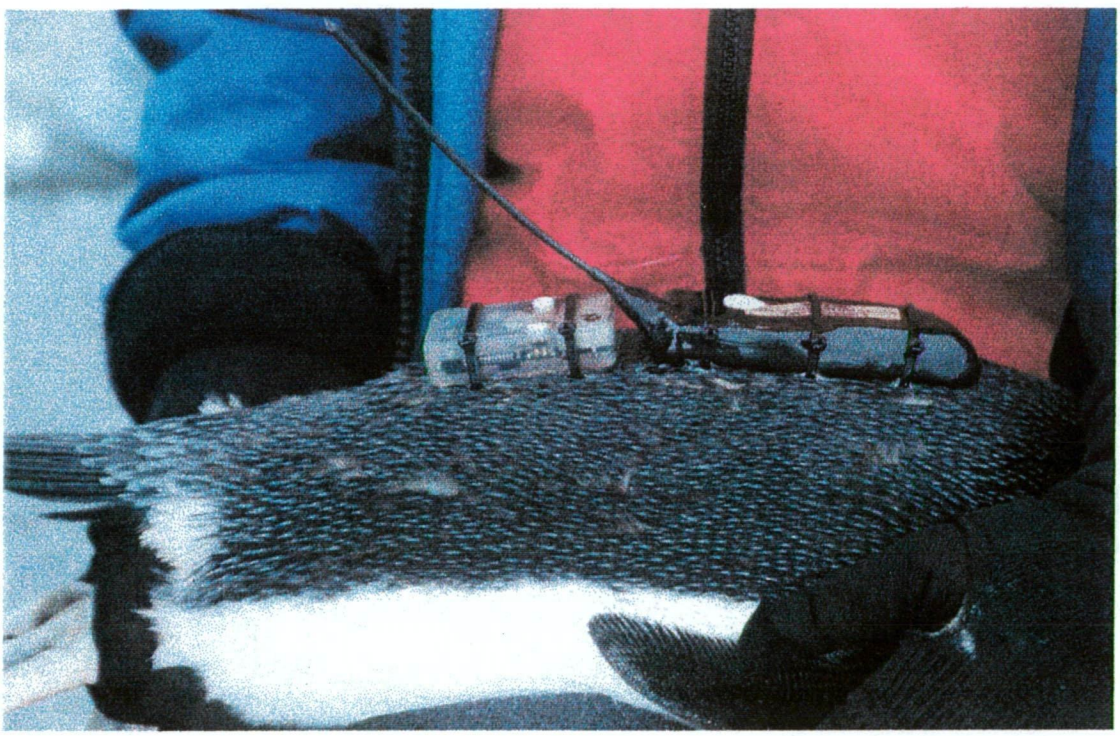


Figure 2.5
Platform terminal transmitter and time depth recorder attached to the lower back of a penguin using Loctite 401™ and cable ties.

CHAPTER 3: IMPLANTED TRANSPONDERS IN PENGUINS: IMPLANTATION, RELIABILITY, LONG-TERM EFFECTS AND APPLICATION TO DEMOGRAPHIC STUDIES.[1]

3.1 INTRODUCTION

Flipper bands have traditionally been used to mark penguins for long-term study, and manual observation methods employed to detect returning individuals. The detrimental effects of bands have been well documented and include mortality during moult (Ainley *et al.* 1983), physical injury (Sallaberry and Valencia 1985), and increased energy expenditure during swimming and foraging (Culik *et al.* 1993; Froget *et al.* 1998). Band loss is also known to occur (Ainley and DeMaster 1980) and returns of some proportion of individuals can be expected to be missed annually (Ainley *et al.* 1983).

The disadvantages of flipper banding have led to the search for alternative marking techniques for penguins and other seabirds. The use of implanted identification transponders has become popular in the livestock industry and in zoos over recent years (Behlert and Willms 1992; D. Spielman, pers. comm.). An automated weighing and identification system has been developed by Kerry *et al.* (1993) for use in the study of Adélie penguins (*Pygoscelis adeliae*) that incorporates implanted transponders and a data-logging device as the means of identifying and recording individual birds as they travel in and out of their colony. Other researchers have also started to use such

[1] Co-authored with Kerry KR and published in slightly different format as "Implanted transponders in penguins: implantation, reliability, and long-term effects" in the Journal of Field Ornithology, 69(2): 149-159. Tables 1 and 2 and associated text have been updated in this chapter from those originally published.

identification systems in colonies of King (*Aptenodytes patagonicus*), Gentoo (*P. papua*), Royal (*Eudyptes schlegeli*), little (*Eudyptula minor)* and Adélie penguins (Gendner *et al.* 1992; McCormick *et al.* 1993; Hindell *et al.* 1996; Olsson 1997; Chiaradia 1998; Ainley *et al.* 1998).

This chapter describes an assessment of the practical use of implanted transponders in Adélie penguins and presents data on mortality rates and transponder durability on the basis of seven years of records from a combined tagging and banding study. Attention is drawn to the potentially serious effects of biofilms on implants that may harbour and release pathogenic bacteria into the bloodstream. The problems of transponder migration and loss are documented, and some possible long-term effects of implants on individuals and populations are discussed. It is important that those intending to utilise implanted transponders as identification markers be alerted to potential problems with these devices.

3.2 METHODS

3.2.1 Study colony and technology

The study commenced in the austral summer of 1991-1992 when 132 breeding adult Adélie penguins at Béchervaise Island (67°35'S, 62°49'E) near Mawson base, East Antarctica were implanted with glass-encapsulated electronic transponders produced by TIRIS™ (Texas Instruments, USA). Sixty of these implanted birds were also fitted with stainless steel flipper bands to enable comparison between banded birds and those carrying transponders alone. A further 85 and 117 penguins received transponders in the 1992-1993 and 1993-1994 seasons respectively (Table 3.1); 40 and 50 of these were also given bands. (Not included in Table 3.1 are an additional 165 birds that received transponders in a season different to that in which they were first flipper-banded.)

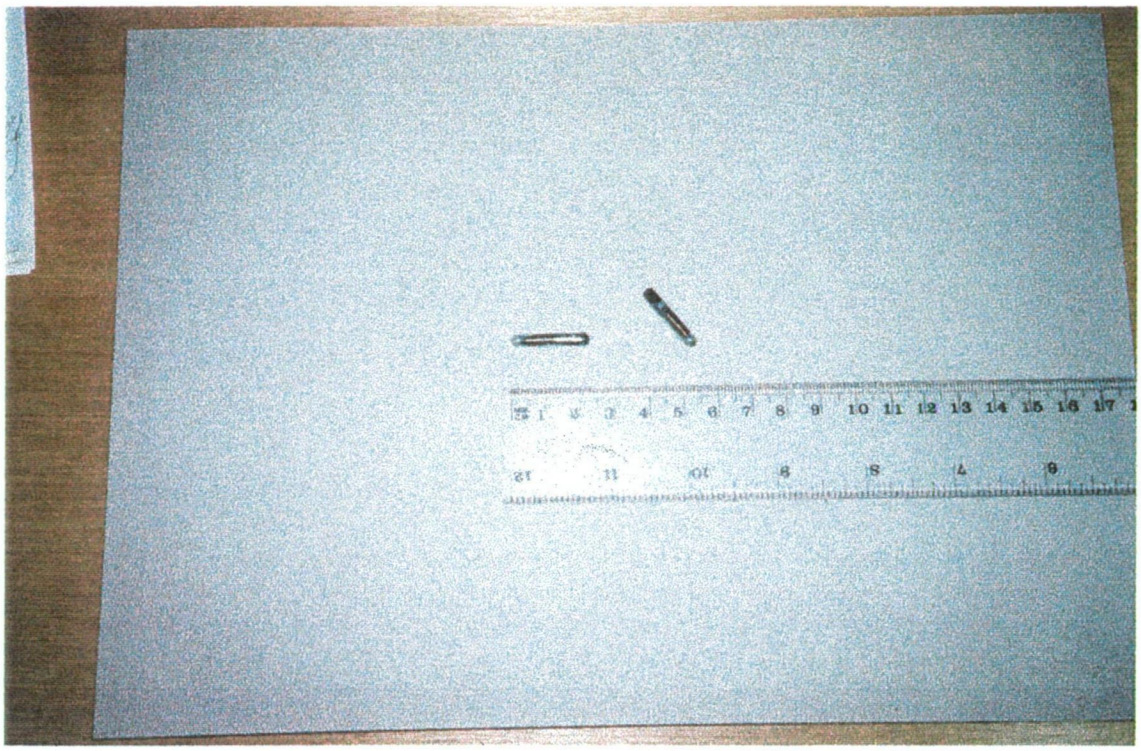


Figure 3.1
Electronic identification transponders produced by TIRIS™ (Texas Instruments, USA). These transponders (23 mm long and 3 mm in diameter) were implanted subcutaneously at the back of the neck or between the shoulder blades.

The transponders implanted in the first two seasons were 30 mm long and 3 mm in diameter; after 1992-1993 a shorter version 23 mm long became available (Fig. 3.1). Use of transponders without banding has continued from 1994-1995 onwards at Béchervaise Island as well as at nearby Verner Island and at Edmonson Point (74°20'S, 165°09'E) in the Ross Sea. Chicks have received transponders (but not bands) in all seasons and locations at a rate of up to 300/yr (except in 1994-1995 at Mawson when starvation caused the whole cohort for that year to die; Kerry *et al.* 1995b). Overall, 1438 adults and 2822 chicks had received transponders by the end of the 1998-1999 breeding season.

TIRIS™ transponders were chosen because they can be detected from a distance of 0.7 m compared to those of other manufacturers that, although smaller, have a shorter read range. Unique identification numbers are transmitted passively from each transponder

in response to electro-magnetic interrogation from a reader. The TIRIS™ system enables automatic detection of birds passing in and out of a fenced colony through a 1 m wide passage using antennae connected to a data-logging system (Kerry *et al.* 1993).

Returns of implanted birds were detected annually by the Automated Penguin Monitoring System (APMS) which ran continuously throughout each breeding season. In addition, the colony was manually checked using binoculars during the incubation period each season for banded birds that had moved to sub-colonies other than those serviced by the APMS. The majority of birds carrying both transponders and bands came from marked nests; these were checked manually with a hand-held transponder detector to pick up any banded birds whose transponders had failed.

3.2.2 Transponder implantation

Transponders were implanted subcutaneously at the back of the neck or between the shoulder blades. These locations were chosen for ease of implantation as they have the most loose skin. Transponders were injected using an applicator provided by Texas Instruments. This device takes cartridges of 10 sterile transponders individually surrounded by iodine gel and allows injection via a large bore needle without direct handling of the implant. The needle was cleaned with iodine solution (Betadine™) between each application to minimise the opportunities for infection.

Transponders were massaged well under the skin to prevent them being lost from the injection wound before it healed. After injection the head was allowed to move freely and the wound rechecked to ensure that the transponder had remained properly under the skin. A cyanoacrylate skin glue (Vetbond™) was trialed as a wound sealant on 40 penguins during 1995 and used routinely thereafter.

The site of transponder implantation was changed in 1996-1997 to a position midway down the back, subsequent to radiographic investigation of the extent of transponder migration. Twenty male Adélie penguins carrying implanted transponders were

radiographed in December 1996 using a Mikasa Atomscope portable X-ray machine driven by a 4.8 KVA generator. Small metal markers were glued temporarily to the feathers on the dorsal and ventral sides of the birds to provide orientation when viewing the radiographs. Each bird was put into a restraining device made of plastic tubing, enabling dorso-ventral and lateral radiographs of the neck and thorax to be taken. The distance and direction of transponder migration were measured for each individual.

3.3 Results and Discussion

3.3.1 Transponder function

3.3.1.1 Types of transponders

A range of identification transponders is now available from different manufacturers. These vary in size, surface coating and distance over which they may be read. The experience reported here is restricted to the TIRIS™ transponders manufactured by Texas Instruments, USA (Fig. 3.1). These transponders are larger than most, however their size enables them to be read over correspondingly greater distances. Identical transponders are being used in studies of little penguins (the smallest of all penguin species) and can be read from outside shallow burrows in sand and through the wood of artificial nest boxes (Chiaradia 1998).

Consideration was taken of the possibility that the glass encapsulating the electronics of the transponder could implode under the pressure of diving and harm the bird. Adélie penguins can dive to 175 m (Whitehead 1989) and Emperor penguins (*A. forsteri*) have been recorded to depths of 534 m (Kooyman and Kooyman 1995). A number of TIRIS™ transponders from different batches were tested to the equivalent of 1000 m depth and showed no damage. These transponders can thus be considered suitable for all penguin species. Other brands of transponders should be pressure tested to such depths before use on deep-diving species.

3.3.1.2 Transponder loss and long-term function

Transponder loss in the first three weeks after injection proved to be a major problem. During the first two years of the study up to 30% of all implants were lost. At that stage transponders were being injected with the needle pointing towards the head as it was easier to part the feathers in that direction. It was discovered that transponders were falling out, assisted by gravity, before the wound healed properly. The problem was exacerbated in thin dehydrated birds during the incubation period (when most tagging was carried out). Regular nest checks enabled detection of transponder losses, and all affected individuals were retagged before the end of each breeding season. It was found that if a transponder was retained for three weeks after tagging then in almost all cases it continued to function into the future.

Transponders are now injected with the needle pointing away from the head and care taken to massage the transponder well under the skin. The hole is rechecked after the bird has retracted its neck to make sure the transponder is not being expelled. Use of 23 mm long transponders instead of the 30 mm ones used in the first two years has also improved the retention rate. However, the receiving antennae on the APMS needed to be more finely tuned to detect reliably these smaller transponders. Transponder loss rates are now only 3-5% and the use of skin glues has lowered this rate further. Only one transponder was lost from 90 Adélie penguins on which Vetbond™ skin glue was used during 1995 and 1996, and the same glue has been used successfully as a sealant for injection wounds in little penguins (Chiaradia 1998). The rate of transponder loss in chicks is unknown; however, there is no reason to expect it to be different to that in adults.

Once a transponder has been successfully implanted and retained for three weeks, it is generally highly reliable. However, some evidence of long-term transponder failure over the years that birds have been carrying these implants to date has been observed. Three hundred and fourteen individuals have now been carrying bands and transponders for up to 7 years. From these individuals five transponders have failed (after 1-4

winters) and eight bands have been lost (after 2-7 years of wear). Two of the birds whose transponders had failed were radiographed and in neither was the implant visible in the neck or thoracic region. It is assumed that in these cases the transponders had migrated right out of the bird, especially since the radiographic survey showed that tag migration over distances up to 5 cm was indeed a common occurrence.

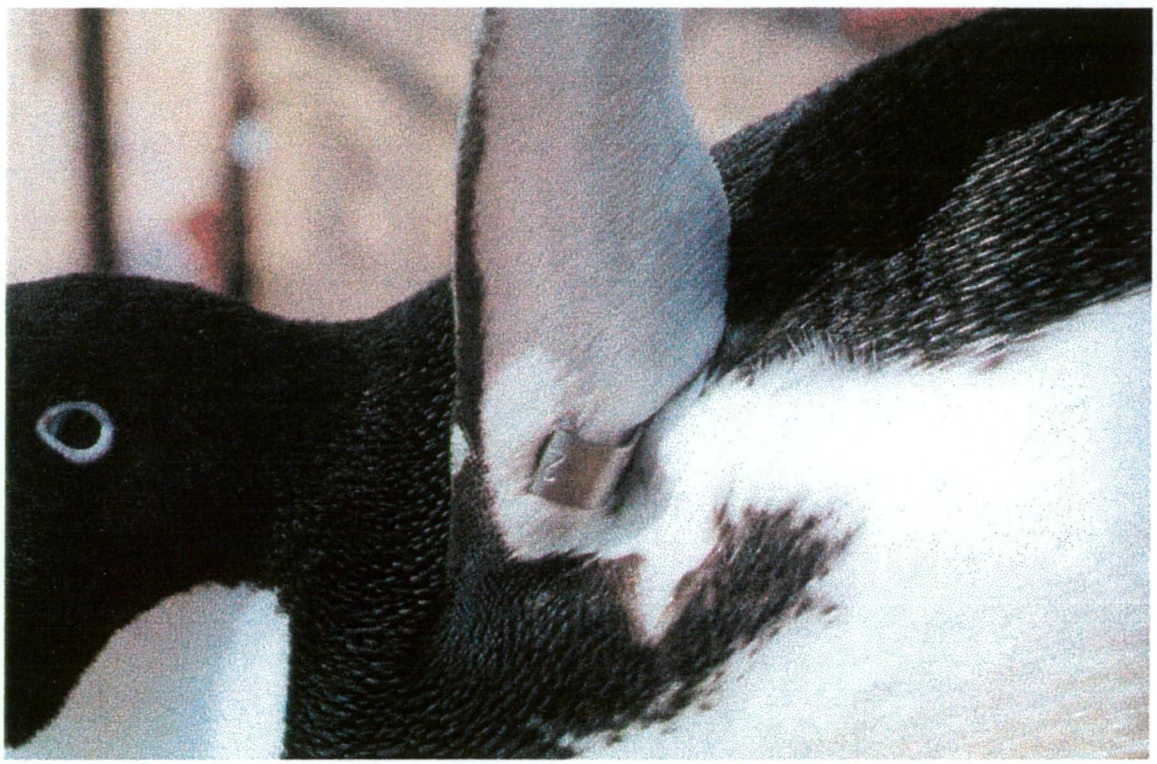


Figure 3.2
Injury due to a flipper band opening and penetrating the radio-carpal joint of an adult Adélie penguin (after 1 year of wear). The band was subsequently removed and, although the joint remained swollen for several months, the bird returned to the colony to breed in the following two seasons.

Numerous flipper bands have been observed to be partially open after one or more seasons of wear (Figs 3.2, & 3.3) and it is considered likely that penguins are opening bands with their bills, thus contributing to band loss and increasing the danger of injuries such as that depicted in Figure 3.2 where the end of the band had penetrated 5 mm into the tissue. Several bands have been removed over recent years because they had opened to such a degree that injury was present or imminent.

3.3.2 Survival rates of adults and chicks

3.3.2.1 Return rates of tagged versus banded adults

The return rates of tagged and banded adults over the first two seasons of this study were reported in Clarke and Kerry (1994). At that stage no differences in survival could be demonstrated between the two groups over the short period. Hindell *et al.* (1996) also found no difference in the survival rates of banded and tagged Royal penguins over a single winter. Over-winter return rates of banded birds have been shown to be lower than those of unbanded birds in the first year following banding for both Adélie (Ainley *et al.* 1983) and king penguins (Froget *et al.* 1998). In comparison, no transponder effects on survival have so far been demonstrated by researchers using such marking devices in penguins (Olsson 1997; Froget *et al.* 1998). Seven years of data were analysed in this study to determine the annual survival rates over each winter of birds banded and tagged during the first three seasons of the programme.

The return rates of birds given transponders alone were greater (78-100%) than those of birds given bands in addition to transponders (63-90%) for almost all seasons following the marking (Table 3.1). The differences were, however, statistically insignificant due to small sample sizes. It can be assumed that all birds that fail to return are dead for four reasons: i) breeders rarely emigrate to other colonies or miss a season, ii) the detection rate of tagged birds using the APMS is extremely high, iii) all unfenced sub-colonies are manually checked rigorously and iv) the observed tag loss rate is less than 3%.

The apparent mortality rate of birds with bands was particularly high over the 1995 winter for all three groups (Table 3.1). This winter followed a summer of severe food shortage (Kerry *et al.* 1995b) and the results shown in Table 3.1 suggest that, when prey is scarce, the extra energy required to swim with a flipper band, quantified by Culik *et al.* (1993), may actually compromise the survival of such birds. There is so far no evidence that implanted transponders increase mortality compared to bands; in fact

indications are that the long-term survival of tagged birds may overall be better than that of those carrying traditional flipper bands (Froget *et al.* 1998; this study).

Table 3.1 Multi-year return rates of Adelie penguins carrying flipper bands and implanted transponders compared to those carrying transponders only. All birds were first banded/implanted as adults and are grouped according to the year in which the band and/or transponder were first applied. Annual differences were not statistically significant.
($\chi_2 < 3.84$, df=1, $p<0.05$)

Birds carrying bands and transponders			Birds carrying transponders only			
	N	%		N	%	difference
Banded and tagged 91-92	60*		Tagged 91-92	72*		
return 92-93	45	75%	return 92-93	56	78%	3%
return 93-94	36	80%	return 93-94	49	88%	8%
return 94-95	31	86%	return 94-95	42	86%	0%
return 95-96	21	68%	return 95-96	34	81%	13%
return 96-97	19	90%	return 96-97	31	91%	1%
return 97-98	17	89%	return 97-98	26	84%	-5%
Banded and tagged 92-93	40		Tagged 92-93	45		
return 93-94	33	83%	return 93-94	40	89%	6%
return 94-95	27	82%	return 94-95	36	90%	8%
return 95-96	17	63%	return 95-96	33	92%	29%
return 96-97	14	82%	return 96-97	29	88%	6%
return 97-98	10	71%	return 97-98	29	100%	29%
Banded and tagged 93-94	50		Tagged 93-94	67		
return 94-95	42	84%	return 94-95	61	91%	7%
return 95-96	28	67%	return 95-96	49	80%	13%
return 96-97	25	89%	return 96-97	45	92%	3%
return 97-98	21	84%	return 97-98	41	91%	7%

* These numbers do not include birds tagged in a season different to that in which they were banded, and thus differ from those published in Clarke and Kerry 1994.

3.3.2.2 Chick survival and return rates

Seven hundred and thirty-three chicks were implanted with transponders between 1992 and 1996. Forty-three percent of these have survived to three or more years of age, the majority first appearing in the colony as 3-yr-olds. The percentages of each cohort known to have survived their first two winters ranged from 41-48%, and 38-45% of each cohort are known to have reached at least 3 years of age (Table 3.2a). Two hundred and thirty-four 3-7-yr-olds were detected in the colony in 1998-1999, and APMS records indicated that some of these were attempting to breed.

Table 3.2 Survival and age-specific return rates of chicks carrying implanted transponders. All chicks died of starvation in 1995. a) Numbers and percentages of each cohort known to survive to minimum ages of 2-7 yrs. b) Pooled survival rate to 3 yrs of age, followed by annual age-specific return rates for pooled cohorts of 3, 4, 5 and 6 yr olds.

a) Chick survival

		1992	1993	1994	1995	1996
Number of chicks tagged:		34	245	261	0	193
number of chicks surviving to age:	2 yr	16	100	126		93
	3 yr	13	99	118		86
	4 yr	10	80	98		
	5 yr	7	65	85		
	6 yr	6	58			
	7 yr	5				
% chicks surviving to age:	2 yr	47%	41%	48%		48%
	3 yr	38%	40%	45%		45%
	4 yr	29%	33%	38%		
	5 yr	21%	27%	33%		
	6 yr	18%	24%			
	7 yr	15%				

b) Chick return rates

	N	%	
0 yr olds	733		
Return as 3 yr olds	316	43%	(5 cohorts pooled)
3 yr olds	230		
Return as 4 yr olds	188	82%	(4 cohorts pooled)
4 yr olds	188		
Return as 5 yr olds	157	84%	(3 cohorts pooled)
5 yr olds	72		
Return as 6 yr olds	64	89%	(2 cohorts pooled)
6 yr olds	6		
Return as 7 yr olds	5	83%	(1 cohort)

The age-specific annual return rates of 3-7-yr-olds have ranged from 82-89% (Table 3.2b), averaging 85%. These figures are within the range for those of banded and/or tagged adults (Table 3.1), as would be expected for birds that are fully mature (Ainley *et al.* 1983).

The overall survivorship of the four cohorts of chicks to 2-7 years of age was greater than that determined by Ainley *et al.* (1983) using banded populations of fledglings. In fact it was also greater than the rate these authors predicted for unbanded fledglings. When examined in detail, the survivorship of fledglings at Béchervaise Island over the

first three years of life (43%) was greater than that of those studied by Ainley *et al.* (1983) at Cape Crozier (24%). During adulthood, however, annual survival rates of known-age birds at Béchervaise Island (82-89%) were lower than those reported for the Cape Crozier population (mean of 89.4% per annum). The greater apparent survivorship of Béchervaise Island fledglings over Cape Crozier birds may be partly due to a degree of bias in the choice of fledglings for transponder implantation at Béchervaise Island where tagging of the smallest chicks has been avoided in order to reduce the expense of wasting tags on birds that may not fledge at all.

Overall, the results of this study indicate that the use of transponders is a reliable alternative to banding for short to medium term demographic studies at least, providing that visual observation is not necessary for the detection of tagged individuals.

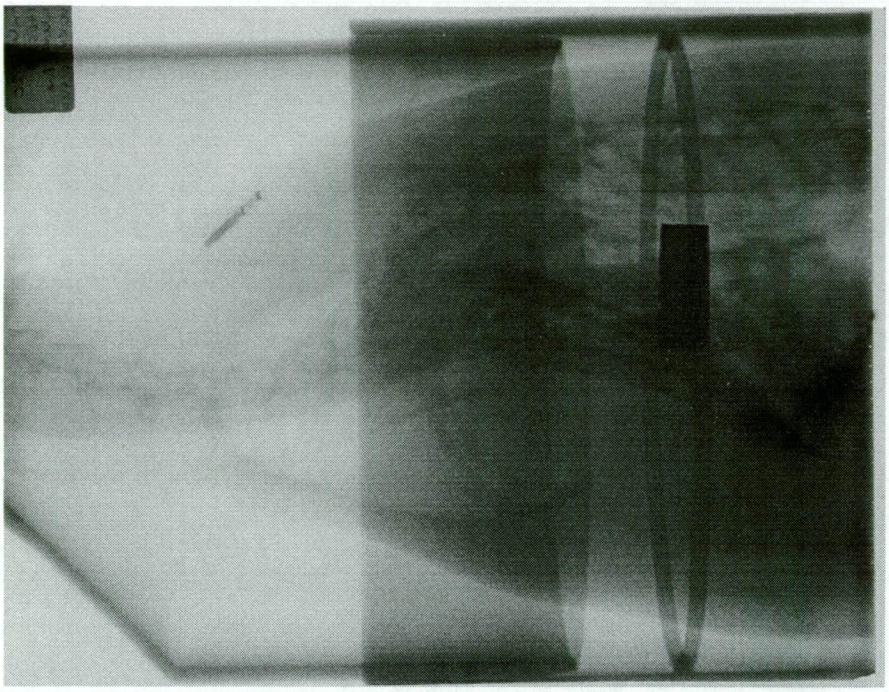
3.3.3 Long term effects

3.3.3.1 Transponder migration

A major problem with implanted transponders is the potential for migration away from the original injection site. Implant migration may or may not cause problems depending on where the device ends up. Larger transponders and those coated with synthetic plastics have been shown to be more likely to migrate than small glass implants (Behlert and Willms 1992).

The transponders used in this study are encapsulated in glass and fairly large compared to other brands (in order to be detected from a distance). In contrast to Behlert and Willms' (1992) suggestion that glass implants are unlikely to move, a proportion of transponders retrieved from penguin chicks killed by skuas were observed to have migrated away from the original site of injection. In most cases the transponders had only migrated slightly, usually to one side or the other of the neck. However, in two chicks transponders were found alongside the trachea and oesophagus.

a)



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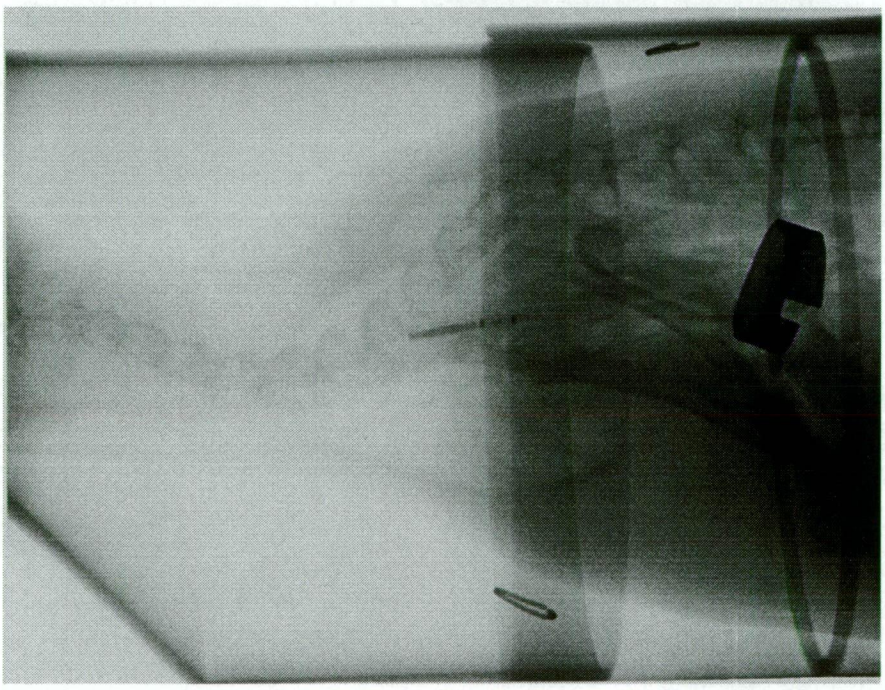


Figure 3.3
Lateral radiographs of a) a penguin into which a transponder has been implanted at the back of the neck and b) a penguin whose transponder has migrated caudoventrally into the thoracic cavity. Flipper bands and externally attached orientation markers are also visible.

Transponder migration over distances of 1-5 cm was demonstrated in 13 of the 20 previously implanted adults examined radiographically in 1996-97. Five birds showed no transponder movement, and in two individuals (identifiable by bands) the transponder no longer existed. Most transponders had moved either laterally or caudoventrally, several into the thoracic cavity (Fig. 3.3). While it is possible that such transponders may never cause damage to surrounding organs, there is some danger that they may obstruct blood flow or damage nerves in the region.

Transponder migration is a cause for concern, despite the fact that the return rates of implanted birds compare favourably to those of banded individuals, and that the birds in which migration has occurred appear healthy. Implantation of transponders farther down the back may reduce the chances of migration into the throat and thoracic cavity. The transponders implanted into adults and chicks during 1996-1997 were injected midway down the back. Subsequent radiography of four individuals showed only slight lateral migration after two months, and no tendency of transponders to move into body cavities. The use of this implantation site has thus been continued.

3.3.3.2 Wound infection and long-term effects of implants

Localised wound infection was not a problem in the days following transponder implantation in either adults or chicks. However, it is possible that minor discharge contributed to the early loss of transponders in some birds during the first fortnight post-implantation. The use of Betadine™ to clean the injector needle and the presence of iodine gel surrounding each transponder help minimise bacterial contamination.

Significant bacterial growth can occur, however, within the biofilms surrounding implants in humans and animals over the long term (Costerton and Lappin-Scott 1989; Deighton and Balkau 1990; Vaudaux *et al.* 1994). Most implant-related infections described in the medical field are associated with devices made from metal and plastic, the surfaces of which tend to erode and facilitate bacterial growth (Deighton and Balkau 1990). Glass is immunologically neutral and less subject to pitting but may chemically

interact with surrounding tissues to form a stabilising capsule (Behlert and Willms 1992).

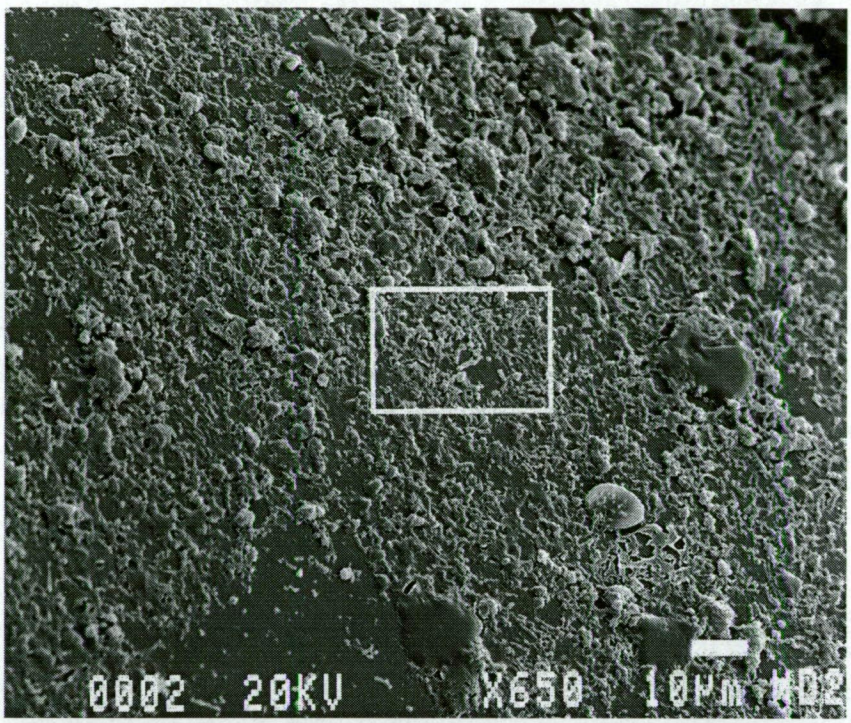
Bacteria associated with implants tend to remain localised, either attached to the implant or encapsulated with it. Occasionally, however, they become detached and disseminate via the bloodstream. The species of bacteria found in biofilms tend to be those normally present on the skin (commonly *Staphylococcus epidermidis* and less frequently *S. aureus*) which, although non-pathogenic in their normal environments, can become virulent when attached to surfaces of implanted materials (Deighton and Borland 1993, Vaudaux *et al.* 1994).

No evidence of chronic localised or systemic infection attributable directly to transponder implants has been observed in birds used in this study. However, such affected birds may be more likely to die at sea than in the colony. The annual survivorship rates reported in this study also provide no cause for concern. Although no adult birds have been killed to check the status of their implants, a number of tagged fledglings killed by skuas were dissected to investigate the tissue reaction around their transponders. In most cases very little tissue reaction was observed ranging from no macroscopic change to encapsulation in thin fibrous collagen layers. These changes correlate well with those reported by, for example, Behlert and Willms (1992) for zoo animals carrying implanted glass transponders.

A notable exception was one implanted transponder removed from a nearly fledged chick that died of causes unrelated to implantation. The transponder was found to be encapsulated and surrounded by a thick layer of purulent material. A heavy biofilm had developed on the glass surface of the transponder (Fig. 3.4). This material contained both cocci and rods, the latter of which appeared to be actively dividing. Culture of the purulent contents of the lesion under both aerobic and anaerobic conditions showed the presence of *Clostridium perfringens*, *C. sordellii* and some unidentified *Bacillus* species. No coccoid organisms could be cultured; presumably the long frozen-storage

time between death of the bird and culture of the lesion had allowed only spore-forming species to survive.

a)



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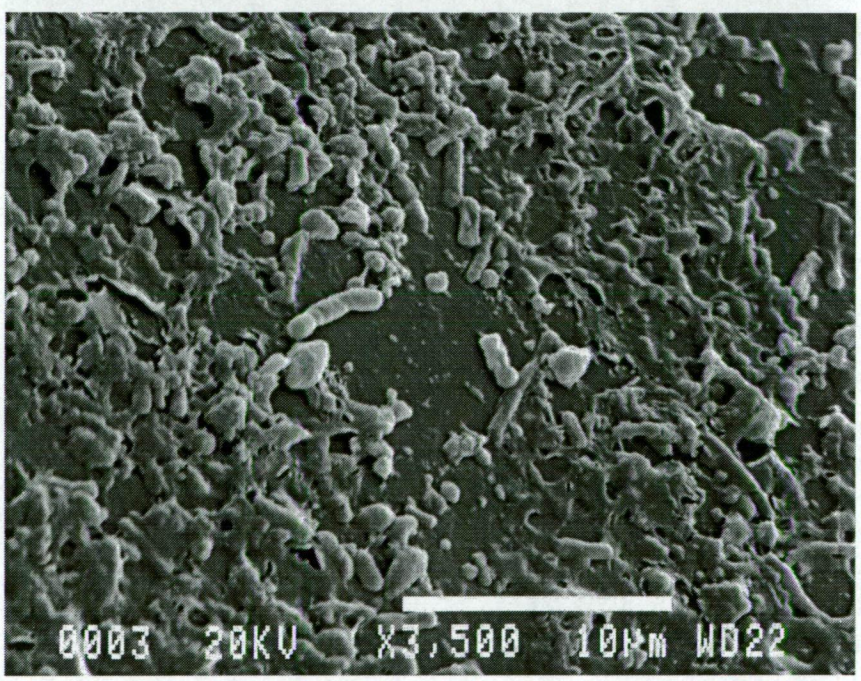

Figure 3.4
Electron micrograph showing bacteria in the slimy biofilm coating the glass surface of an encapsulated transponder removed from a fledgling.

It is not yet known what long-term effects may result from transponder implantation. The population of Adélie penguins in this study could normally be expected to live to up to 20 years of age (Ainley *et al.* 1983). If biofilm formation and persistent bacterial infections are common then it may be found that transponder implantation actually shortens the life expectancy of penguins to some degree. The level of such an effect may be difficult to determine, especially as only banded birds are available for comparison and these are also likely to be adversely affected by their identification markers.

Further research is required to quantify and reduce the incidence and effects of both biofilm development and transponder migration, especially as such risk factors may limit the use of implanted transponders in endangered or long-lived species. Although transponder migration may be difficult to prevent, introduction of bacteria into the implantation site can be minimised. Cleansing of the skin at the injection site with 70% alcohol will help prevent incorporation of micro-organisms into the capsule around the implant, as will disinfection of the implantation device between individuals. In the case of the fledgling described earlier, the transponder had been unintentionally implanted within muscle tissue, a factor that may have exacerbated the tissue reaction. Glass-coated implants are likely to be safer than those with plastic surfaces and care should be taken to ensure that each transponder is positioned subcutaneously in a location from which it is unlikely to migrate towards vital organs.

CHAPTER 4: SEX DIFFERENCES IN ADÉLIE PENGUIN FORAGING STRATEGIES[2]

4.1 INTRODUCTION

Adélie penguins (*Pygoscelis adeliae*) live and breed around the entire Antarctic continent (Woehler 1993) and are known to feed on a wide range of organisms including krill, fish, squid and amphipods (Volkman *et al.* 1980; Lishman 1985a; Puddicombe and Johnstone 1988; Ridoux and Offredo 1989; Kerry *et al.* 1994). Their foraging ranges during the post-hatch stages of chick rearing vary between locations; those breeding on the Antarctic Peninsula travel relatively short distances (14--60 km) to feed mainly on krill (Lishman 1985a; Trivelpiece *et al.* 1987; Wilson *et al.* 1989b; 1994) while those breeding on the continent tend to travel further (up to 120 km) and feed on a variety of organisms from over the shelf as well as in deep water (Paulin 1975; Puddicombe and Johnstone 1988; Ridoux and Offredo 1989; Kerry *et al.* 1994; Ainley *et al.* 1998).

Environmental conditions within the foraging ranges of Adélie penguins also differ between locations. Penguins rearing chicks on the Antarctic Peninsula feed in a region of seasonal pack ice (Trivelpiece *et al.* 1987; Chappell *et al.* 1993b) while those in some parts of East Antarctica forage under the fast ice throughout the entire breeding season (Watanuki *et al.* 1994). Adélie penguins in many regions such as the Mawson coast (Kerry *et al.* 1995a; this study) and the Ross Sea (Ainley *et al.* 1998; this study) feed both under the pack ice and in open water. Such variations in the overall foraging behaviour of Adélie penguins are indications of the capacity of these birds to modify

[2] Co-authored with Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S and published in Polar Biology 20:248-258. The addendum (section 4.5) was written following subsequent data analysis and has not yet been published in any form.

their foraging strategies to take advantage of the spatial and temporal distributions of prey in the regions where they breed.

It has been assumed until now that both male and female Adélie penguins have similar foraging strategies, especially since they show little sexual dimorphism. Chappell *et al.* (1993b) showed that each sex contributes differently in terms of energy budget to the rearing of offspring, with females expending 16% more energy during the post-hatch period than males (although using 38% less energy during courtship and incubation). Although it has been noted that females spend 15% more time away from the nest than males during chick rearing (Chappell *et al.* 1993b), the relationship of energy budgets to foraging strategies has not been examined. Most dietary studies of Adélie penguins have dealt only with unsexed birds (Lishman 1985a; Puddicombe and Johnstone 1988) or have been carried out in the region of the Antarctic Peninsula where krill is the only prey species consumed (Volkman *et al.* 1980).

Much of the research described in this chapter was carried out in the Prydz Bay region of East Antarctica where Adélie penguins feed on a wide range of prey species over a large foraging range (Kerry *et al.* 1994) and where the distribution of prey species is patchy and sometimes even extremely scarce (Hosie and Cochran 1994; Kerry *et al.* 1995b). Penguins in this location sometimes have difficulty finding enough food for their chicks, and their breeding success is often lower than at most other breeding sites (Lishman 1985b; Whitehead *et al.* 1990; Kerry *et al.* 1993, 1995b). It could be expected that under such conditions mechanisms to reduce foraging competition between the sexes would be utilised wherever possible.

4.2 METHODS

4.2.1 Breeding colonies and study birds

The study was carried out at two locations: Béchervaise Island (67°35'S; 62°48'E) near Mawson Station in East Antarctica and Edmonson Point (74°21'S, 165°10'E) in Terra Nova Bay on the Ross Sea. Béchervaise Island is a long-term monitoring site under the CCAMLR Ecosystem Monitoring Program (CEMP) where Australia has carried out research into Adélie penguin breeding biology and foraging ecology on a colony of 1800 breeding pairs since 1990. A monitoring site at the similar-sized Adélie colony at Edmonson Point was established during the 1994-95 season and identical studies have been initiated there to allow comparison between a colony with access to deep water off the edge of the continental shelf (Béchervaise Is) and a colony which forages exclusively in shallower waters (Edmonson Pt).

Transponder tags encoding individual identification numbers were subcutaneously implanted into 384 females and 389 males at Béchervaise Island between 1991 and 1996, and into 230 females and 182 males at Edmonson Point during the 1994-95 and 1995-96 breeding seasons. Further details on transponder implantation methods and effects have been detailed in Chapter 3. Birds carrying transponders were detected by an Automated Penguin Monitoring System (APMS) consisting of a weighbridge, tag reader and data logging system as they entered and left their colonies (see Chapter 2 and Kerry *et al.* (1993) for more detailed descriptions on the use of this system). All penguins were sexed by cloacal examination at the time of transponder implantation, and those on study nests marked with different coloured dyes during the incubation period if regular nest observations were to be required during chick rearing.

The results reported in this chapter were obtained from the guard and crèche stages of the 1991-92 to 1995-96 breeding seasons at Béchervaise Island, and from the same stages in 1994-95 and 1995-96 at Edmonson Point.

4.2.2 Foraging trip durations

Post-hatch foraging trip durations of breeding males and females from 150 marked nests were extracted from APMS records collected at Béchervaise Island during the 1991-92 to 1994-95 seasons, and at Edmonson Point in 1995-96 (Table 4.1). All recorded foraging trips were verified against data from twice daily nest observations to ensure that transponder detection was reliable. At Edmonson Point in 1994-95 (the season prior to installation of an APMS) round-the-clock observations of 120 nests over a ten-day period during the guard stage were used to provide similar data on foraging trips.

Foraging trip durations were grouped by sex within either the guard or crèche stages of chick rearing for each location and season, and frequency distributions generated for each group (Fig. 4.1). Numbers of trips and numbers of penguins involved are shown in Table 4.1. The distributions of trip durations were highly skewed overall and those for individual penguins within a breed stage were generally not normally distributed. To test for male-female differences without being concerned about the distributions for individual penguins, randomisation tests (Manly 1997) were carried out separately for the guard and crèche stages of chick rearing for each of the stage-season combinations at each location. The method used was as follows:

The mean duration for all males was calculated giving equal weight to all observations irrespective of how many were available for each penguin. Similarly the mean was calculated for all females. The difference D_1 (female-male) was also calculated. A randomised set of data was calculated on the null hypothesis that the labels "male" and "female" are independent of foraging times. This was done in two stages. First the nests with records for only one tagged penguin (male or female) were considered. The labels "male" and "female" were randomly allocated to the penguins in these nests, keeping the total number of each sex the same as in the original data. Next the nests with both a male and a female were considered. The labels "male" and "female" were switched with a probability 0.5. Mean values and their difference (D_2) were calculated as before. These steps were repeated 4999 times to generate randomised differences D_2,

D_3, ..., D_{5000}. The original difference, D_1, was then significantly different from zero on a two-sided test if it was either one of the largest 2.5% or one of the smallest 2.5% of the full set of 5000 differences. The probability of this happening by chance if there is no male-female difference is 0.05. The procedure is easily modified to allow tests at other levels of significance. A similar procedure was used to search for evidence of variance difference associated with sex.

The error structure in the data was complex, with sampling variation associated with repeated foraging trips by one penguin, differences among penguins, and possibly differences among penguins in different nests. These complications can be allowed for by bootstrap resampling (Dixon 1993; Efron and Tibshirani 1993) which was carried out to generate standard errors (Table 4.1). Bootstrap resampling was carried out as follows: First, nests with only one tagged penguin (male or female) were sampled with replacement to give the same number of nests in the bootstrap sample as for the original data. For each chosen nest the foraging durations for the penguin were then resampled to give the same number of durations as for the original data. Second, the nests with two tagged penguins were sampled with replacement to give the same number of such nests as for the original data, and each penguin given a new set of trip durations by resampling from the ones available for it. In all cases a resampled penguin kept its original sex, and the number of recorded trips per penguin was also kept equal to the values for the real data. These steps were repeated 4999 times. The standard error of any parameter such as the female mean duration or the difference between the male and female mean durations is estimated by the standard deviation of the estimates calculated from the bootstrapped data.

Estimated mean trip durations and their standard errors were used to test for effects associated with the sex of the penguins, the six location-season combinations, the two stages (guard and crèche) and the interaction between these factors. This was done by fitting the corresponding three-factor model to the data using GLIM (Francis *et al.* 1993) with the weight given to any mean value being the reciprocal of its estimated variance. The female-male differences were also analysed in a similar manner, although in this

case there were only the two factors (location-season combination and breed stage) and their interaction to be considered.

The distributions of foraging trip durations at Béchervaise Island tended to show a bi-modal pattern (Fig. 4.1a). Trips were categorised as long or short on the basis of these distributions, using 40 hours as the cut-off duration. Randomisation analyses to test whether birds of one sex were more likely to make long or short trips than the other were run on the foraging duration data using a dummy variable = 1 for durations over 40 hr, and 0 otherwise. (The sample means of this variable thus corresponded to proportions (P) of long duration trips.)

4.2.3 Foraging locations

The foraging locations of breeding birds were determined by satellite tracking at Béchervaise Island during each of the 1991-92 to 1995-96 breeding seasons, and during 1994-95 at Edmonson Point. Male and female penguins carried platform terminal transmitters (PTTs) during both the guard and crèche periods. The PTTs were ST-6 and ST-10 models produced by Telonics Ltd. (USA). They were tapered at the front and packaged in resin by Sirtrack Ltd. (NZ) to withstand diving to 200 m. Packaged weights were 160 g and 90 g respectively. See Kerry *et al.* (1995a) and Chapter 2 for further details on attachment and deployment. Transmissions were detected by National Oceanic and Atmospheric Administration (NOAA) satellites and the positions of birds calculated through the Argos (France) location system. ST-6 PTTs were used in the first two seasons and replaced by the smaller ST-10 version from 1994-95 onwards. Significant effects of such devices on foraging trip duration and breeding success, although measurable during the incubation period, were not able to be demonstrated at the Béchervaise Island study site post-hatch in seasons when food supplies were plentiful (Clarke and Kerry 1994). However, it is likely that the high variability in foraging trip duration demonstrated by the penguins at Béchervaise Island during chick rearing masks any significant effects on trip length given the small sample sizes available for analysis.

Locations were obtained from 21 male and 17 female birds which carried out totals of 56 and 37 foraging trips respectively over five breeding seasons at Béchervaise Island. A further seven males and five females were tracked at Edmonson Point during 1994-95 for 18 and 13 foraging trips respectively.

Foraging trips at Béchervaise Island were divided into two categories on the basis of the tracks (Table 4.2). Local trips were those with maximum distances of less than 20 km, while distant trips were to locations greater than 40 km from the island. Most birds in the latter group travelled between 80 and 120 km from the colony to the continental shelf break, which is commonly represented by the 1000 m depth contour. Proportions of local and distant foraging trips of males and females during both guard and crèche stages for each year were compared using Fischer exact tests.

4.2.4 Diet

Five stomach samples were collected each five days from breeding penguins of known sex throughout the chick rearing period at both locations during each season. Birds chosen for stomach flushing were captured at random as they returned from the sea to their nests in colonies other than those serviced by the APMS. They were sexed by cloacal examination prior to collection of stomach contents using the water off-loading method of Wilson (1984), with multiple flushes as described in detail in SC-CAMLR (1997) and Chapter 2. In addition, 19 of the birds that carried satellite trackers also had stomach contents removed.

Stomach samples from the 1991-92 to 1994-95 seasons at Béchervaise Island and from 1994-95 and 1995-96 at Edmonson Point were analysed according to the revised CEMP Standard Methods (SC-CAMLR 1997) and wet weights of each of the major dietary components recorded. Results from the guard and crèche stages were pooled for males and females to determine mean percentages by mass of dietary components for each sex.

4.3 RESULTS

4.3.1 Foraging trip durations

Frequency distributions of foraging trip durations of males and females during four seasons at Béchervaise Island and two seasons at Edmonson Point are shown in Figure 4.1 a&b. These results are for the guard and crèche periods separately except for the 1994-95 season at both locations when data were only collected during the guard stage. All data are derived from APMS records apart from the 1994-95 durations from Edmonson Point, which were manually collected. Mean foraging trip durations and standard errors for males and females during both guard and crèche stages in each season are shown in Table 4.1, along with sex differences.

Male birds at both locations made shorter trips on average than did females, especially during the guard stage when differences were significant to at least the 1% level for all seasons analysed (randomisation tests). Mean foraging trip durations during the guard stage ranged between 25-36 hr for males and 31-73 hr for females, and all mean values were significantly different from those expected if foraging duration was independent of sex (Table 4.1). Mean crèche stage trip durations ranged between 16-39 hr and 22-45 hr for males and females respectively. Sex differences at Béchervaise Island during this latter stage were less significant than during guard; differences remained highly significant at Edmonson Point throughout the one season for which data were available from both stages (Table 4.1).

The results of tests for effects associated with location-season combinations, stages (guard and crèche) and the interaction between these factors were not significant, except for a difference at the 5% level between season-location combinations due to the large female-male difference at Béchervaise Island in 1994-1995. Females in this latter

season carried out trips almost twice as long as in the other years studied (Table 4.1). The overall picture at both locations therefore was for males to make consistently shorter foraging trips than females, especially during the guard stage, during every season for which data were analysed.

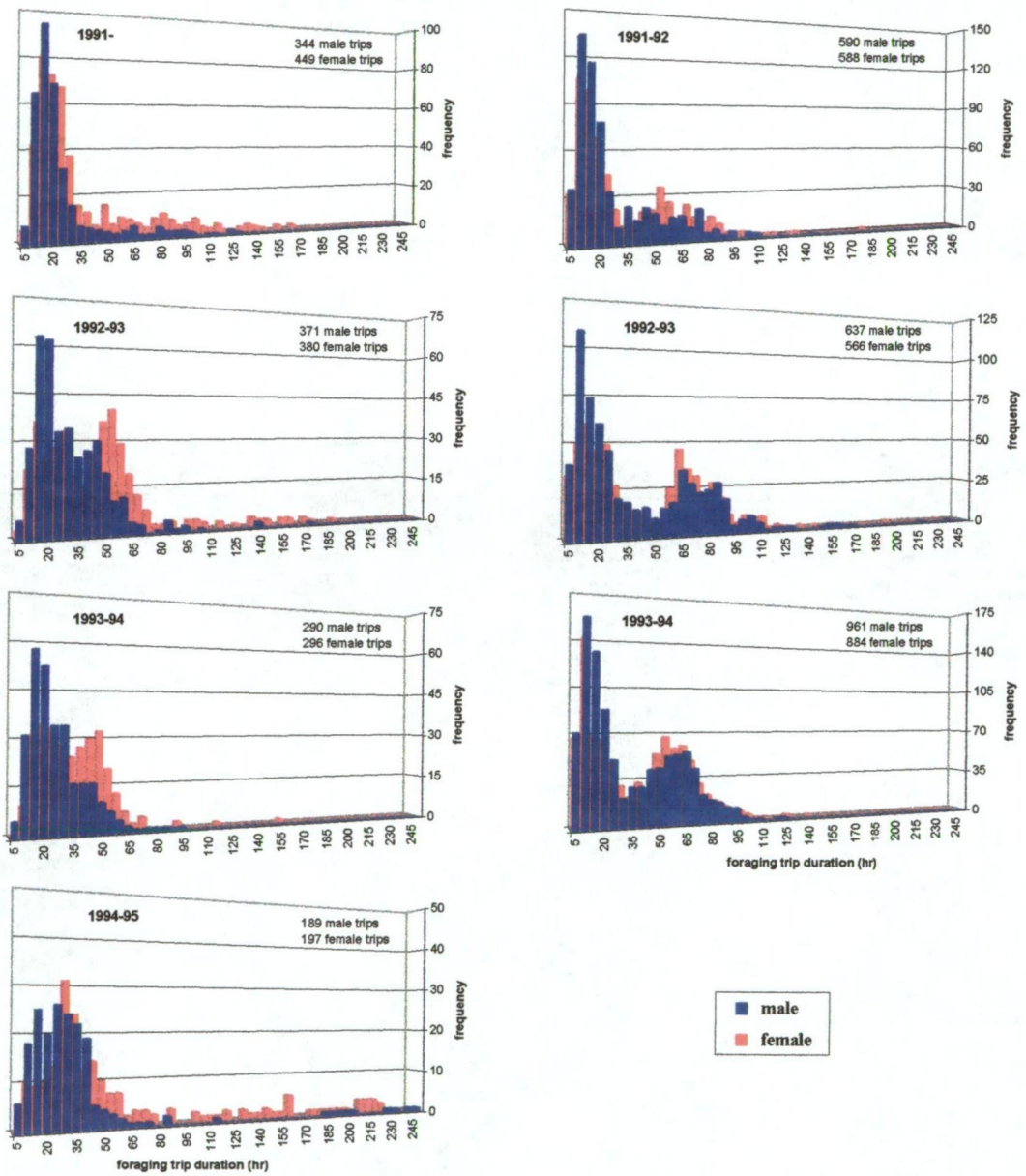

Figure 4.1a)
Frequency histograms of male and female foraging trip durations during the guard and crèche periods for the 1991-92 to 1994-95 seasons at Béchervaise Island.

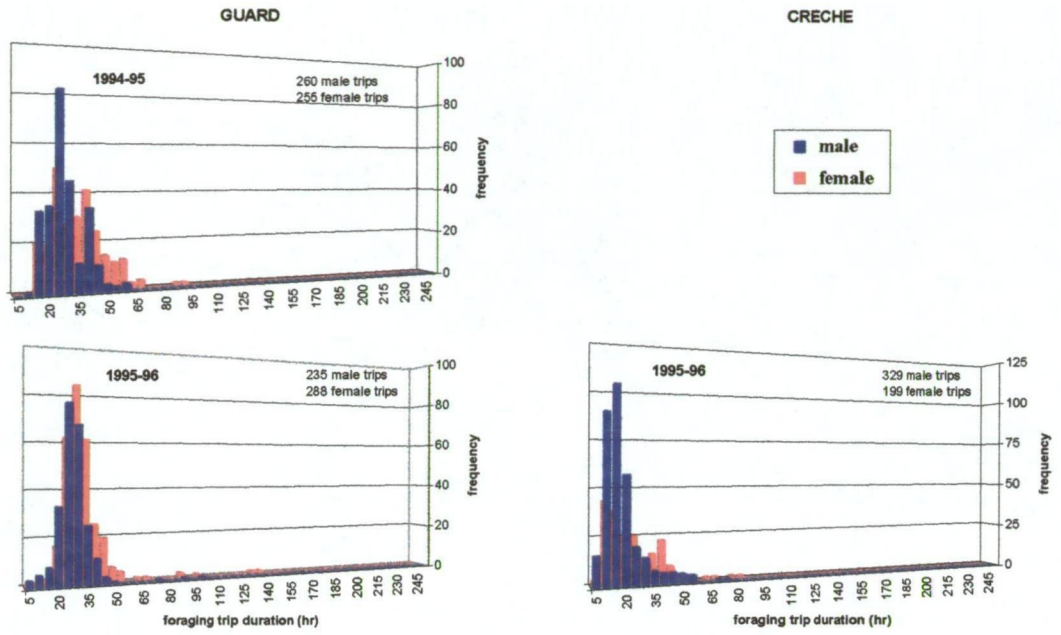

Figure 4.1b)
Frequency histograms of male and female foraging trip durations during the guard and crèche periods for the 1994-95 and 1995-96 seasons at Edmonson point.

A bi-modal pattern was apparent in the distributions of foraging trip durations at Béchervaise Island (Fig. 4.1a). This was most obvious during the crèche stage, although two peaks were also present in most female distributions during the guard stage. Results of two-sided tests showed that during the guard stage females were about twice as likely as males to make long trips (1% significance level for 1991-92; 0.1% significance level for the other three seasons). The distribution of foraging trips of females did not change greatly between the guard and crèche stages, but for males the proportion of long trips increased during crèche. No bi-modal pattern of trip durations was obvious at Edmonson Point.

Table 4.1 Mean foraging trip durations for male and female Adelie penguins during guard and creche stages of chick rearing for a number of seasons at two locations. Means that are significantly different from values expected if foraging duration was independent of gender are indicated with asterisks. Female-male differences are also provided. Standard errors were determined by bootstrapping as described in the text.

			Guard								Creche							
Location	Season	Sex	Mean Trip Duration (hr)	SE		female-male difference (hr)	SE		trips N	birds N	Mean Trip Duration (hr)	SE		female-male difference (hr)	SE		trips N	birds N
Bechervaise	91-92	m	26.1	2.9	**	9.4	3.9	**	344	57	26.4	1.7	**	5.0	2.4	*	590	46
		f	35.5	2.8	*				449	63	31.4	1.9	*				588	52
Bechervaise	92-93	m	32.5	3.2	***	12.0	3.9	***	371	74	39.4	2.3	*	5.1	3.2	*	637	71
		f	44.5	2.4	**				380	71	44.5	2.4	*				566	66
Bechervaise	93-94	m	24.8	1.3	**	10.0	2.1	***	290	71	34.1	1.4		3.6	2.4		961	77
		f	34.8	1.7	***				296	77	37.7	1.9					884	76
Bechervaise	94-95	m	36.2	4.6	***	37.2	8.2	***	198	67	chicks dead							
		f	73.3	7.9	***				209	76	chicks dead							
Edmonson	94-95	m	26.0	0.9	***	5.5	1.3	***	260	94	na							
		f	33.5	1.3	***				255	97	na							
Edmonson	95-96	m	25.3	0.9	***	5.6	1.5	***	235	55	15.7	0.9	***	6.2	1.9	***	329	35
		f	30.9	1.2	***				288	61	21.8	1.7	***				199	35

Significance: * 5% level ** 1% level *** 0.1% level (using Randomization Tests)

4.3.2 Foraging locations

Foraging trips determined by satellite tracking from Béchervaise Island were divided into local and distant categories for both the guard and crèche stages of the chick rearing period (Table 4.2). Maps of both types of trip are shown in Figure 4.2. Most distant trips extended as far north as the continental shelf break, while the end points of local trips tended to be scattered within 10 km of the colony.

Table 4.2 Numbers of trips to local and distant foraging grounds made by penguins tracked by satellite from Bechervaise Island over five seasons.

	Number of trips									
Season	1991-92		1992-93		1993-94		1994-95		1995-96	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Guard Period										
Distant	1	3	0	0	0	3	1	2	1	2
Local	2	0	4	2	12	7	4	4	7	2
Creche Period										
Distant	3	1	2	0	3	5	0	0	0	0
Local	9	0	2	0	5	6	0	0	0	0

Overall, 90% of the satellite tracks obtained from males during the guard stage were to destinations less than 20 km from the colony. Only 40% of the tracks obtained from females at the same time were this short, the majority being 80 to 120 km in range. However, both males and females made similar proportions of local to distant trips (67% vs. 50%) during the crèche period.

There were no distinct trip types discernible from the tracking study at Edmonson Point. It was noted, however, that three individual males each made 3-4 successive trips of shorter distance than the majority of those made by other birds in the study, whilst none of the females showed such a tendency.

The ratios of local to distant trips made by male birds from Béchervaise Island during the guard stage were not significantly different to those of females in any one season (Fischer exact tests, P-values ranging from 0.200-1.000); neither were differences significant during the crèche stage (P-values between 0.308-1.000). There was, however, at both locations a relationship between foraging location and trip duration:

birds travelling greater distances remained at sea for longer than those which foraged closer to the colony. Foraging trip durations and maximum foraging distance from the colony were obtained for 70 trips made by birds carrying PTTs from Béchervaise Island between 1991-92 and 1995-96. Foraging trip duration and distance travelled were highly correlated (Pearson Product Moment Correlation, r=0.860, P<0.001). The same was true for 25 trips at Edmonson Point during 1994-95 (r=0.931, P<0.001).

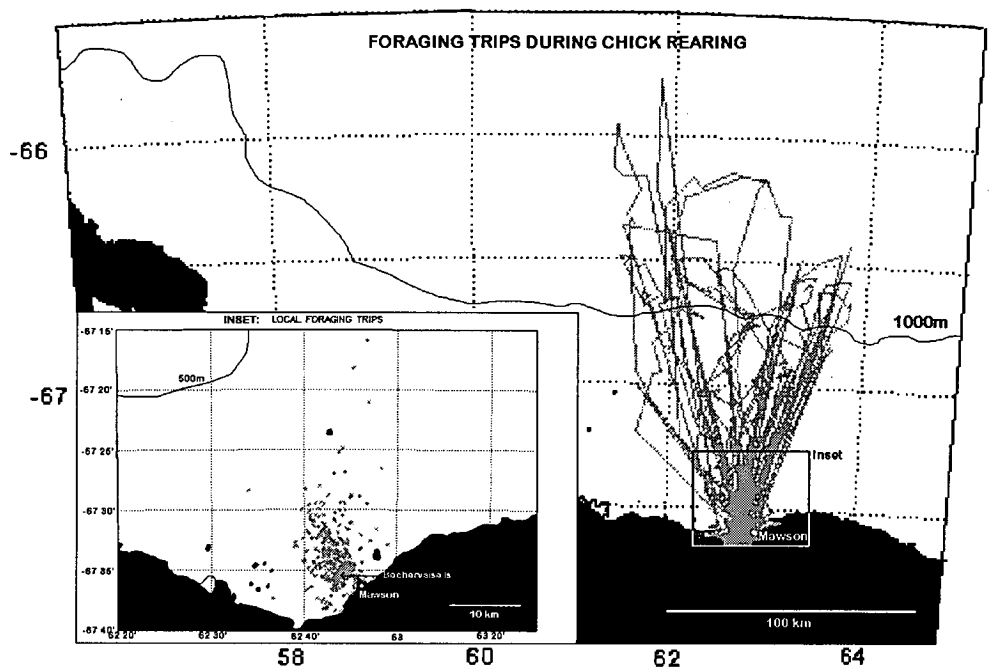

Figure 4.2.

Satellite tracks from trips made by Adélie penguins. Main figure: distant trips (>40 km) over the 1991-92 to 1995-96 seasons at Béchervaise Island; inset: positions of satellite fixes on local trips (<20 km) over the same five seasons. The continental shelf break (1000 m depth contour) is 100 km from the colony at its nearest point.

4.3.3 Diet mass and composition

Mean meal mass and diet composition of male and female penguins during the guard and crèche periods for 1991-92 to 1994-95 at Béchervaise Island are shown in Figure 4.3a, and similar data for Edmonson Point during 1994-95 and 1995-96 are shown in Figure 4.3b. *Euphausia superba* was the most common euphausiid species captured by birds at Béchervaise Island, while at Edmonson Point the smaller *E. crystallorophias* was most often eaten. *E. superba* is usually restricted to shelf-edge zones (Hosie and Cochran 1994), although it is occasionally found in shallower waters associated with the pack ice during early summer (O'Brien 1987). *E. crystallorophias* is most commonly found over the continental shelf. The major fish species consumed by Adélie penguins in the both regions were *Pleuragramma antarcticum* and *Trematomus newnesi*. The former is found both over the shelf and in deeper water, while the latter is more common in the shallower neritic zone (Williams and McEldowney 1990; Hosie and Cochran 1994).

Although the overall composition of the Adélie penguin diet varied between seasons, krill (mostly *E. superba*) comprised a greater proportion of the diet of female penguins than that of male birds at Béchervaise Island in all seasons analysed except for 1994-95. This held true for both the guard and crèche periods (Fig. 4.3a). Males on the other hand tended to eat greater amounts of fish and amphipods than did female birds. These sex differences, although consistent, were however not statistically significant (z-tests). Euphausiids also comprised a greater proportion of the diet of female birds at Edmonson Point during the guard stage (Fig. 4.3b), although at this location during the crèche stage males ate more krill than females (differences again not statistically significant).

The mean meal mass of female birds from Béchervaise Island during the guard period when they were making greater numbers of long trips to shelf-edge destinations was greater than that of males in all seasons except 1994-95 (Fig. 4.3a). Males, however, always brought back more food than females during the crèche stage despite their

continued preference for fish and their generally shorter trip durations (Fig. 4.3a, Table 4.1). The sex differences in meal size were, however, not statistically significant (Three-Way ANOVA, P=0.645). There were also no statistically significant differences in meal mass among seasons (P=0.066) or breed stages (P=1.000) at Béchervaise Island, nor interactions between season and breed stage (P=0.427), season and sex (P=0.717) or breed stage and sex (P=0.185) using Three-Way ANOVA and Tukey pairwise multiple comparison procedures.

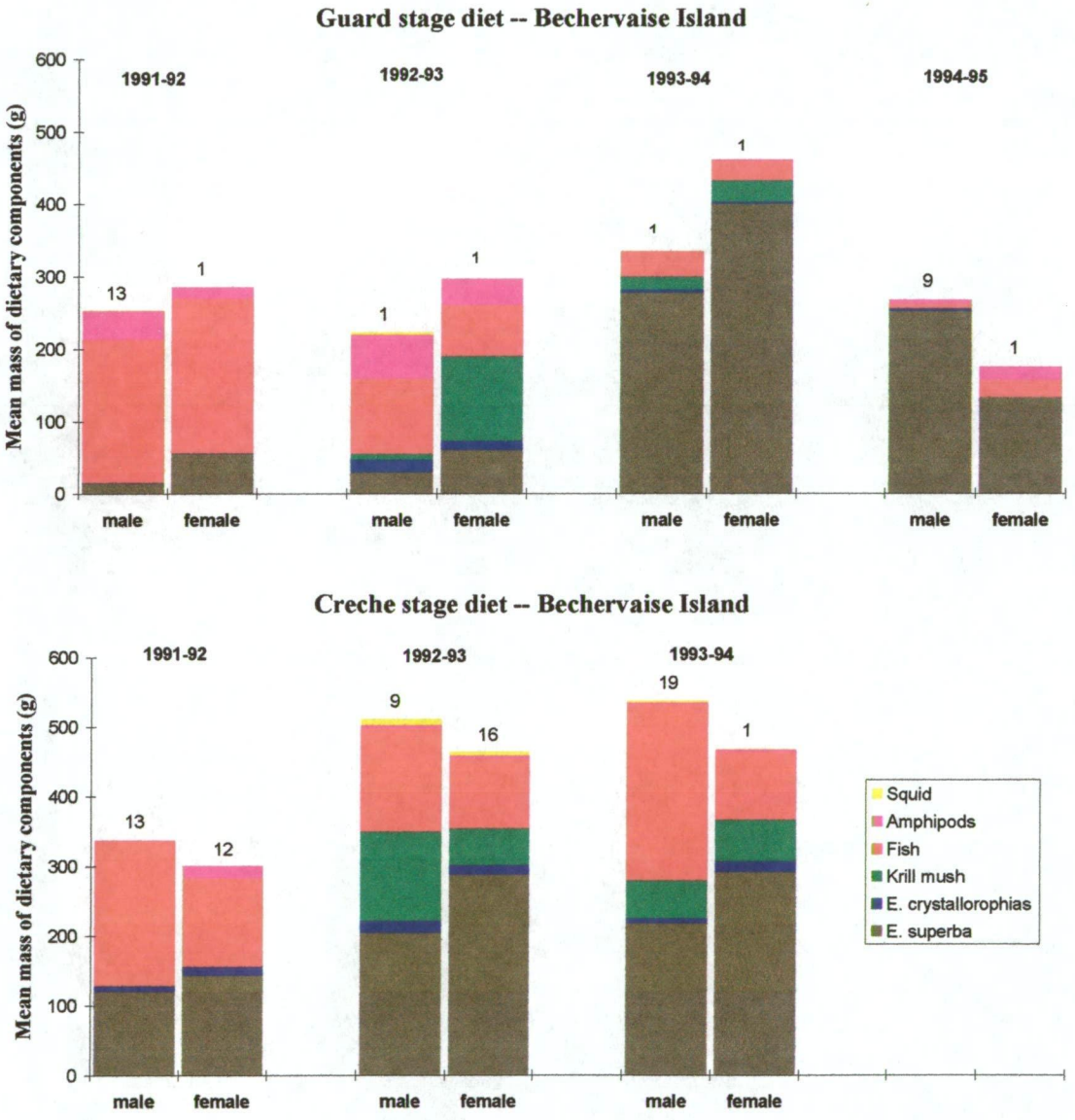

Figure 4.3a)
Mean meal mass and diet composition of male and female Adélie penguins during the guard and crèche stages at Béchervaise Island in the 1991-92 to 1994-95 breeding seasons. The number of birds pooled per group is shown above each column.

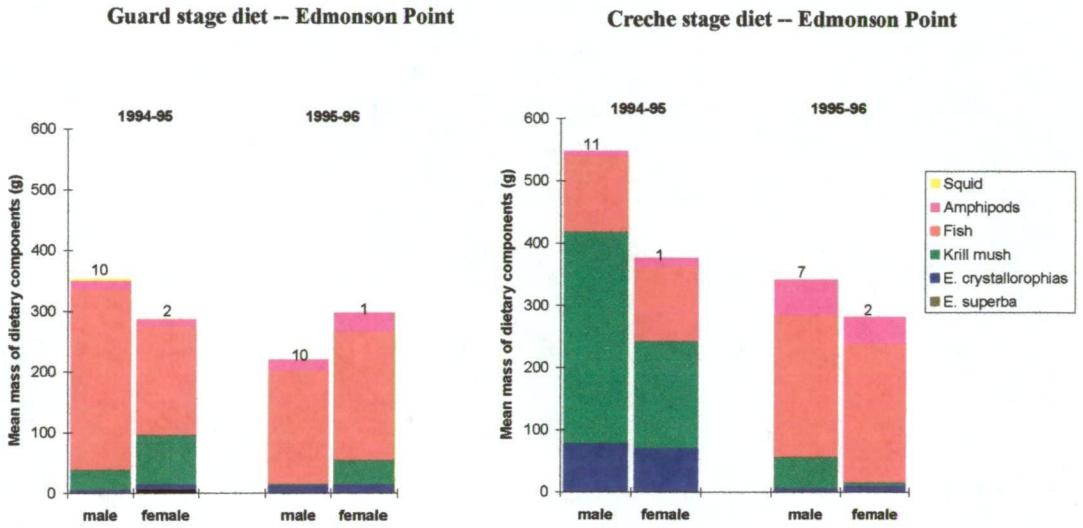

Figure 4.3b)
Mean meal mass and diet composition of male and female Adélie penguins during the guard and crèche stages at Edmonson Point in 1994-95 and 1995-96. The number of birds pooled per group is shown above each column.

The proportion of krill in the diet of birds at Béchervaise Island was greatest during 1993-94, and meal sizes were also largest in this season. 1993-94 was the season of highest breeding success in the colony (Table 4.3) and was also the only year that *E. superba* was found in inshore regions (as determined from stomach-flushed birds which had carried satellite trackers).

Table 4.3 Breeding success of penguins at Béchervaise Island during the 1991-92 to 1994-95 breeding seasons.

Season	1991-92	1992-93	1993-94	1994-95
Breeding success (chicks per pair raised to crèche age)	0.75	0.80	1.06	0.02

At Edmonson Point males brought back larger meals than females during the crèche stage, and also during the guard stage of 1994-95 (Fig. 4.3b). Sex differences were significant (Three-Way ANOVA, P=0.05), as were differences in mean meal mass

values between seasons and breed stages ($P<0.001$ for each). There were also statistically significant interactions between season and sex ($P=0.026$) and breed stage and sex ($P=0.03$), again using Three-Way ANOVA and Tukey pairwise multiple comparison procedures.

Nineteen of the Béchervaise Island birds from which stomach contents were obtained had carried satellite trackers and made trips of known duration. A general relationship between trip duration, location and diet was found in the majority of these birds: five of the seven birds which made local trips of short duration (i.e.: less than 40 hours) consumed fish and amphipods, while the stomachs of 11 of the 12 birds which made longer trips to the edge of the continental shelf contained mainly krill.

4.4 Discussion

The results reported here demonstrate some previously unrecognised differences between the foraging strategies and time budgeting of male and female Adélie penguins, particularly in the guard stage of the chick rearing period. Although associations between foraging trip durations, stage of breeding and diet have been described for Adélie penguins in general (Puddicombe and Johnstone 1988; Whitehead 1989; Kerry *et al.* 1994; Coria *et al.* 1995), this is the first detailed examination of sex differences in foraging to be carried out in this species.

Throughout this study there were consistent differences between male and female breeding adults in trip duration, foraging location and diet at two widely separated sites and over a number of years. Female Adélie penguins made significantly longer foraging trips than males, ranged greater distances during the guard stage and tended to consume larger quantities of krill at the time when chicks were small. Males during the guard period made shorter journeys to closer foraging grounds and fed more extensively on fish.

On the surface it appears that during the early part of the chick rearing period the female member of a pair works harder to feed the offspring by travelling longer distances and bringing back more krill than does her mate. When time at sea and meal mass are taken into account, the fact that foraging trip durations differ significantly between the sexes while meal sizes do not suggests that the provisioning rate of males (food mass brought back per hour at sea) may actually be greater than that of females. Preliminary analysis of weight data derived from the APMS indicates that this may indeed be the case (unpublished data). However, meal size may not truly represent provisioning rate during the guard stage because males spend longer in the colony than do females at this time and are thus likely to use a greater proportion of their stomach contents to support themselves rather than their chicks. This is especially probable during the early stages of chick rearing when male birds may still be recovering from their long courtship and incubation fasts over which they lost a greater percentage of their body mass than did their mates.

Chappell *et al.* (1993b) showed that male Adélie penguins put more of their reproductive effort into courtship and incubation than did their mates (63 v. 39 MJ), while female birds expended more energy during the chick rearing period than did the males (36 v. 31 MJ). It was also noted that male birds spent on average 15% more time at the nest during chick rearing than their partners. These calculations agree well with observations at Béchervaise Island on the differences in foraging strategies between the two sexes during chick rearing. The work of Chappell *et al.* (1993b), carried out at Anvers Island on the Antarctic Peninsula, indicates that sex differences in the foraging strategies of Adélie penguins may be widespread amongst the species even in locations where their diet consists almost exclusively of krill.

The results described in this chapter suggest that by the crèche stage male birds had recovered sufficiently from their pre-breeding fast to collect greater proportions of the food requirements of their growing offspring. They travelled further, fed more frequently than during the guard period and brought back larger meals. Despite these changes, males continued throughout the breeding season to show a greater preference

for fish than did females and to make shorter foraging trips on average than their mates. This suggests that a certain level of partitioning of foraging activity between the sexes persists throughout the season, possibly driven by the energetic requirements elucidated by Chappell *et al.* (1993b) which were found to carry through from guard into the crèche stages (*albeit* to a lesser extent).

Further, the observed differences in foraging strategies and dietary preference may contribute towards a reduction in intraspecific competition between male and female birds despite the lack of obvious sexual dimorphism in the Adélie penguin (Agnew and Kerry 1995). Intraspecific differences in dietary composition have been demonstrated in another pygoscelid penguin, the gentoo (*P. papua*), by Volkman *et al.* (1980) who found that male gentoo penguins consumed 23% more fish than females, despite the lack of sex differences in energy expenditure or foraging trip duration demonstrated for this species (Davis *et al.* 1989). Adélie penguins in the report of Volkman *et al.* (1980) ate only euphausiids; however, it was noticed that male birds consumed significantly smaller euphausiids than did females, perhaps due to foraging in a different location or at different depth strata. This was in contrast to Ainley and Emison (1972) who found that male Adélie penguins consumed larger krill than did females. Differences in depth utilisation of males and females have been recorded for penguins at Béchervaise Island (see Chapter 5); however, these appear to be related to foraging location rather than to sex *per se*.

Sex differences in dietary preference may become particularly important when food supplies are short as a means of both reducing intraspecific competition and of maximising the chances of one member of the pair locating food for the chicks without excessive waste of overall search effort. Such strategies will only become readily apparent in situations where birds have access to a variety of food types over a wide ranging area such as is the case at both Béchervaise Island and Edmonson Point. Intraspecific differences are likely to be most emphasised in years where spatial distributions of the various prey species are different but their overall availabilities in terms of mass and density are similar.

The degree of intraspecific partitioning of foraging observed in this study may simply be a result of the requirement of males to replenish their body reserves following their greater energy expenditure during courtship and incubation (Chappell *et al.* 1993b) by therefore travelling shorter distances and feeding on local prey species. However, this does not explain why females, even when food appears to be locally abundant, still travel further afield; particularly as the males seem able to provide meals of similar (sometimes greater) size for their chicks with less apparent effort when local food supplies are plentiful. It may be that the birds know from experience that the shelf edge is normally a predictable region of food supplies (particularly krill), and females are energetically more capable of travelling that far in the early stages of chick rearing than are their mates.

Personal observations indicate also that the slightly larger and more aggressive male birds tend to defend their nests more vigorously against skua attack and human approach than do their mates during the guard period. Nest defence is an important factor in chick survival during the time that the young are most vulnerable to predation and disturbances in the colony, and it makes sense that the more aggressive parent should spend most time on the nest at this stage. Male Adélie penguins are more territorial than females during courtship, arriving first at the beginning of the season and establishing and defending their territory (Penny 1968; Ainley *et al.* 1983). The bond between a male and his nest may thus be greater than that of his mate, leading to a greater tendency for the male to defend his territory throughout the season. Prior to egg-laying males have been shown to be more aggressive towards intruders than females, although during incubation aggressiveness of both sexes was similar (Spurr 1974). Males were slightly more aggressive during the guard stage than females, although the differences were not statistically significant (Spurr 1974). Males have also been shown to spend more time at the nest than females during the guard period (Ainley *et al.* 1983; Chappell *et al.* 1993b). It is thus possible that such behavioural differences between the sexes contribute to the tendency for male birds to forage locally in preference to travelling further afield.

An understanding of the sex differences in foraging strategies is important for long-term monitoring studies (such as the CEMP) whose objectives include the detection of effects of variations in krill availability on parameters related to the breeding success of penguins. This study has demonstrated annual variations in the importance of krill in the diet of Adélie penguins at two locations and a tendency for female birds to depend more heavily upon euphausiids, particularly in the guard period when females may be collecting the majority of their offspring's food requirements. It is important not only to know how much the birds depend on krill overall, but also to determine at which stages in the breeding season krill is most important to the penguins and how the availability of other prey species affects the foraging strategies of these birds.

At present the revised CEMP Standard Methods (SC-CAMLR 1997) only require that diet be analysed during the crèche period. The results presented in this chapter suggest that information on the guard stage diet may be most vital, as this is when intraspecific differences in foraging strategies are greatest. The guard stage may also be the time when chicks are most likely to die from starvation (Boersma and Stokes 1995; Kerry *et al.* 1995b). These results also emphasise the importance of knowing the sex of the birds being sampled, particularly in locations where *E. superba* is not reliably a major prey species.

4.5 ADDENDUM: FORAGING DECISION AND RESOURCE ALLOCATION.

Analysis of APMS-derived weight data subsequent to publication of this chapter has provided supporting evidence for an alternative explanation of the observed gender differences in foraging behaviour to those described in the discussion above.

In section 4.4 it was suggested that a possible reason behind the observation that males carried out shorter trips than females during the guard stage was that they were recovering from their greater expenditure of energy during courtship and incubation. This was based on the findings of Chappell *et al.* (1993b) who showed that male Adélie penguins put more of their reproductive effort into courtship and incubation than did their mates (63 v. 39 MJ). The work of Chappell *et al.* (1993b) was carried out at Torgersen Island on the Antarctic Peninsula where the penguins averaged 2.8 foraging trips each during the incubation stage, and where the body mass of males did not change significantly from the end of the second incubation trip onwards. The incubation stage of Adélie penguin breeding chronology is somewhat different at Béchervaise Island. Females and males each carry out a single long foraging trip during incubation. The males usually return only a few days before hatching of the chicks after which both sexes forage alternately, as described in section 4.3.

An analysis of weight data collected by the APMS from 63 male and 68 female Adélie penguins during the 1992-93 season showed that the departure weight of males decreased by more than 1000 g over the guard stage (Fig. 4.4a). Departure weights of females, on the other hand, decreased by approximately 500 g over the same period (Fig. 4.4b). Weights of both sexes increased slightly (approximately 200 g) during the crèche stage (Fig. 4.4c&d). Preliminary analyses of APMS data from other seasons indicate that this pattern is consistent between years. Thus it does not appear, in terms of body mass at least, that male Adélie penguins at Béchervaise Island have any requirement to regain energy stores during the early stages of chick rearing. An alternative hypothesis for the observed gender differences in foraging strategies is therefore required.

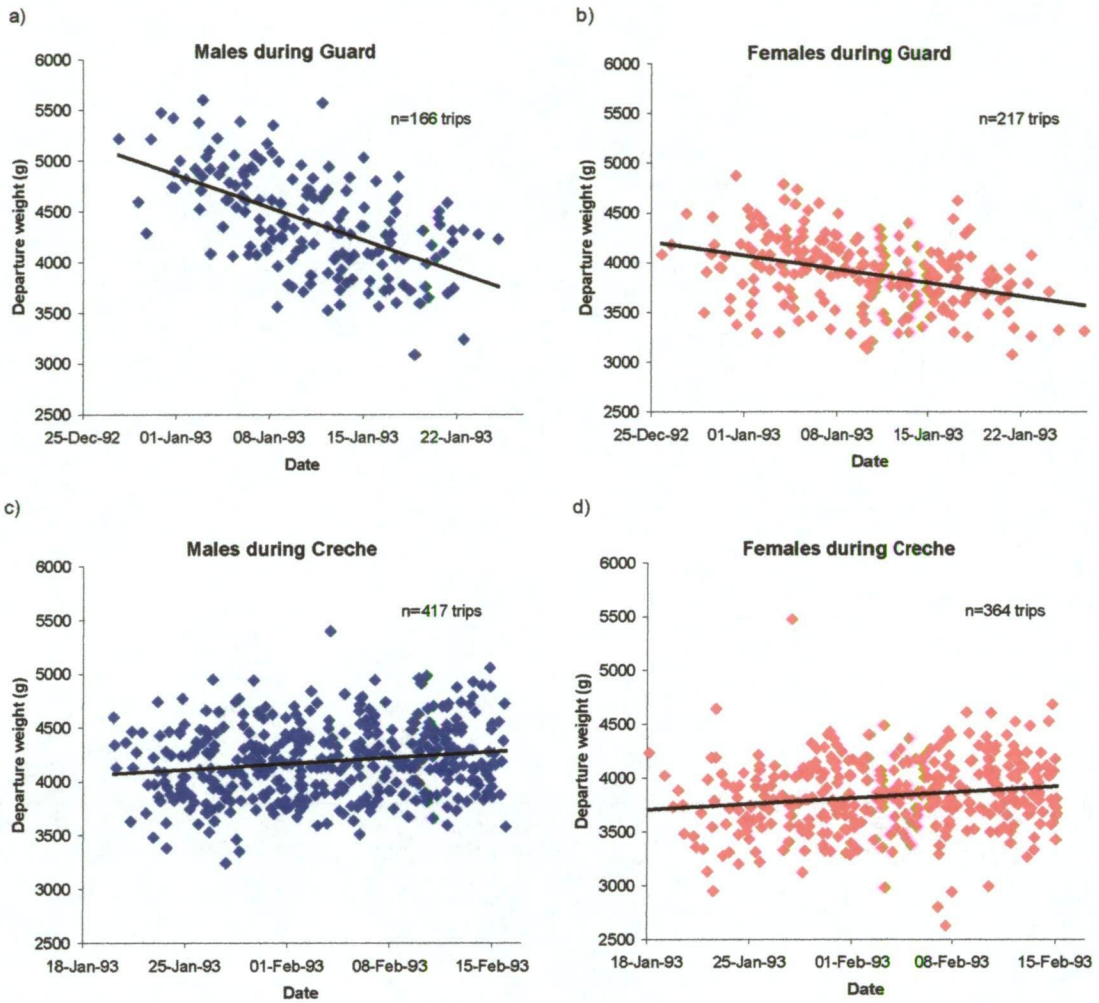

Figure 4.4
Scatter plots of departure weight versus date for penguins carrying out foraging trips to provision chicks: a) males and b) females during the guard stage; c) males and d) females during the crèche stage.

Some species of flying seabirds have been shown to carry out alternate long and short foraging trips during the time that they are feeding chicks (Weimerskirch *et al.* 1994, 1997; Weimerskirch 1998). This twofold foraging strategy has been suggested to be the result of a trade-off between the allocation of food to chicks and storage of parental body reserves. Wandering albatrosses (*Diomedea exulans*) and sooty shearwaters (*Puffinus griseus*) both rely on long foraging trips in distant waters to restore their own body condition, but carry out short trips closer to their colonies to provision their chicks

(Weimerskirch *et al.* 1997; Weimerskirch 1998). Chicks benefit from the frequent feeds resulting from short trips, but these are at the expense of the parents' stored energy resources. Prey capture rates appear to be greatest for birds foraging in distant, more productive, waters. In addition, flight costs may be reduced on long trips due to increased opportunities to soar (Weimerskirch *et al.* 1997). The decision to forage close to or far from the colony appeared in sooty shearwaters to be under the sole control of adult body condition, with long trips initiated when body mass approached a threshold level (Weimerskirch 1998).

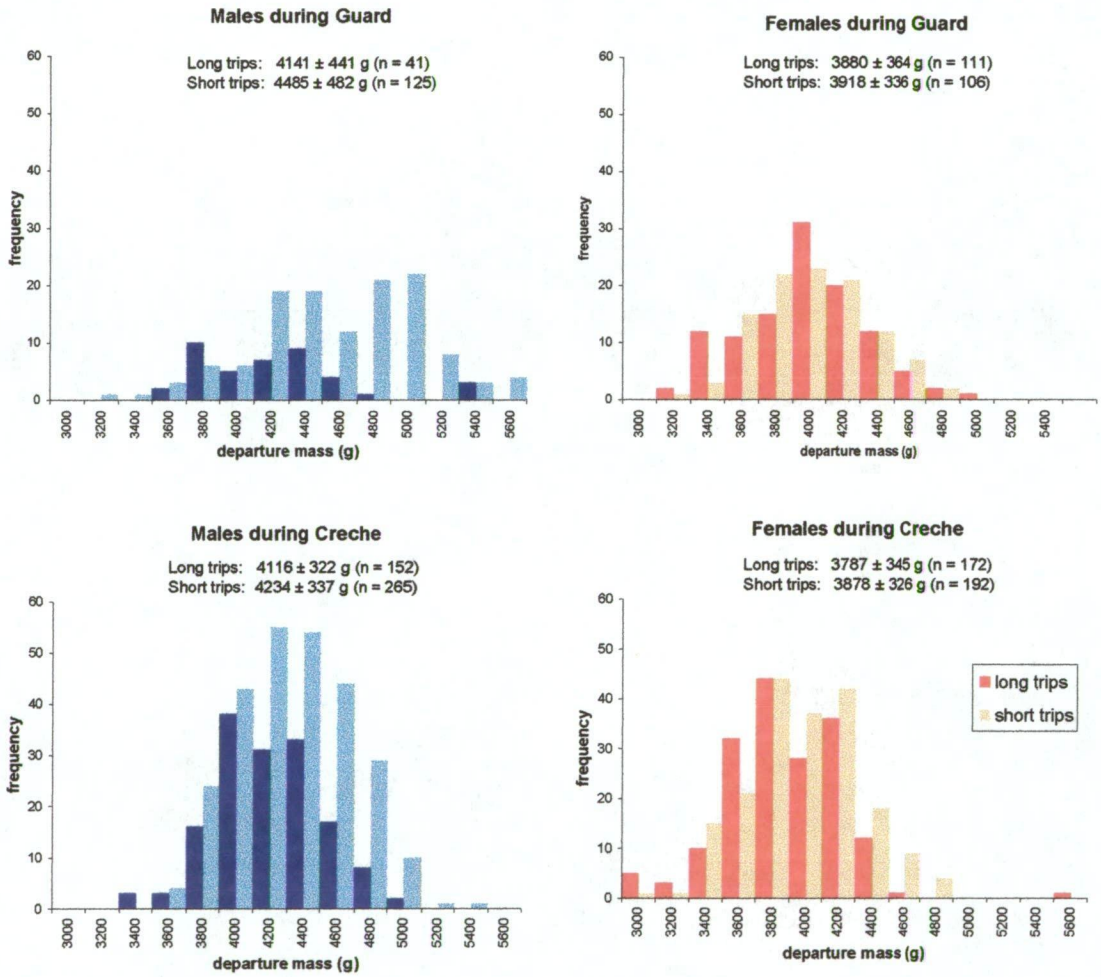

Figure 4.5
Frequency distributions of the weights of male and female penguins prior to departure on foraging trips of long or short duration during the guard and crèche stages of 1992-93. Mean values (± 1 SD) are shown for long and short trips within each group.

The 1992-93 APMS-derived weight data were used to investigate whether the alternate long and short foraging trips carried out by Adélie penguins at Béchervaise Island might be another example of a trade-off between the allocation of food to chicks and maintenance of parental body condition. Departure weights of individually identified males and females carrying out long and short trips (> or < 40 hr respectively) were compared during both the guard and crèche stages of that breeding season. Frequency distributions and mean values of these weights are shown in Figure 4.5 for all trips recorded.

Mean departure weights were compared without taking bird identity into account using unpaired t-tests. Significant differences in departure weight prior to long *versus* short trips were present for males during both guard and crèche stages (t=-4.050, t=3.499 respectively; $p<0.001$) and for females in the crèche stage only (t=-0.08, p=0.425 for guard; t=-2.585, p=0.01 for crèche).
Two-way analyses of variance were used to compare mean departure weight values among different individuals prior to trips of long or short duration. Only birds that carried out at least three trips of both long and short duration were included and males and females were analysed separately. Guard and crèche stages were combined for these analyses in order to obtain large enough sample sizes.

Results showed, for both sexes, that departure weights prior to long trips were significantly lighter than were those prior to short trips (F=18.887, F=11.723 for males and females respectively; $p<0.001$). Departure weights also differed significantly among individuals (F=9.144, F=10.369 for males and females respectively; $p<0.001$) but there was no significant interaction between individual identity and choice of trip type (F=0.910, p=0.6 for males and F=1.119, p=0.310 for females).

Further research is required, using larger data sets on individual birds, to determine conclusively whether gender differences in Adélie penguin foraging trip durations are driven by the same trade-off between the allocation of food to chicks and storage of

parental body reserves as has been described for flying pelagic seabirds. The evidence from this preliminary analysis suggests that Adélie penguin foraging decisions may indeed be under this kind of control. Males are sufficiently heavy at the start of the guard stage to afford to lose weight for a few weeks, enabling them to carry out short foraging trips to provide frequent feeds for their chicks at the expense of their own body reserves. Females, on the other hand, cannot afford to lose so much body condition and must thus forage in regions where prey is abundant in order to maintain their own energy reserves as higher priority. The edge of the continental shelf is known to be a zone of high productivity (Hosie 1991; Hosie and Cochran 1994; WG-EMM 1999) where birds are presumably able to forage most efficiently. Once chicks reach crèche age the body condition of male parents has lowered sufficiently for them to be driven to forage more frequently in such regions. Frequent feeding is also of lesser importance to the chicks when they are older; especially once both parents are free to forage simultaneously.

The edge of the continental shelf lies between 80 and 120 km offshore from the Mawson coast (Kerry *et al.* 1995a). Satellite tracking studies have shown that penguins can cover the distance between their colony and the shelf edge in as little as 24 hours (unpublished data). A return trip, including bringing back krill for the chicks thus takes at least two days, and often longer. By foraging close to the colony birds can ensure that their chicks are fed more frequently than would be the case if all birds travelled to the shelf edge to feed. It appears, however, that the yield of local foraging trips within the coastal neritic zone is insufficient for birds to maintain their own body reserves in addition to bringing back regular meals for their chicks. Thus, foraging effort is partitioned between the sexes, with the males accepting a net rate of negative energy gain to provide regular meals for their offspring during the guard stage. Birds of both sexes carry out longer trips to regions of higher or more predictable prey availability once their body reserves become sufficiently low that replenishment is required. It is likely that a threshold body mass exists below which birds initiate long foraging trips. Breeding success of Adélie penguins in the Mawson region is thus likely to be affected

not only by the availability of local and shelf-edge prey, but also by the body condition of the birds, particularly males, during the early guard period.

CHAPTER 5: VARIATIONS IN ADÉLIE PENGUIN DIVING BEHAVIOUR IN RELATION TO STAGE OF BREEDING, FORAGING TRIP DURATION AND FAST ICE EXTENT.[3]

5.1 INTRODUCTION

Studies of Adélie penguin diving behaviour have shown that this species forages at a variety of depths at different locations (eg: Wilson *et al.* 1989a, 1991; Whitehead 1989; Chappell *et al.* 1993a; Watanuki *et al.* 1993). Although Adélie penguins feeding in areas of pack ice and open water tend to reach greater maximal depths than do those foraging under fast ice, the majority of dives in most locations are relatively shallow compared to the physiological capabilities of these birds (Wilson *et al.* 1989a; Naito *et al.* 1990; Chappell *et al.* 1993a; Watanuki *et al.* 1993, 1997).

Most research has been carried out on either the Antarctic Peninsula where foraging ranges are generally less than 60 km and birds are feeding in pack ice or open water (Wilson *et al.* 1989a, 1991; Chappell *et al.* 1993a), or in regions of persistent fast ice where birds are known to feed close inshore (Naito *et al.* 1990; Watanuki *et al.* 1993). Adélie penguins at these sites depend almost exclusively on krill (*Euphausia superba*) for sustenance. Few investigations have occurred at locations where Adélie penguins forage at a variety of distances from their colonies, or where fast ice conditions change over the chick-rearing period. Neither has the diving behaviour of Adélie penguins that feed extensively on species other than krill been studied in any detail.

Investigations of the foraging behaviour of Adélie penguins along the Mawson coast in East Antarctica have shown that birds feed at a wide range of distances from the colony on a variety of different prey organisms (Kerry *et al.* 1994, 1995a). Fast ice in the

[3] Co-authored with Kerry KR and Wynen L, and submitted for publication.

Mawson region is extensive at the start of the summer, reduces rapidly during the stage when chicks are small and is normally gone completely by the time chicks are in crèches. The demonstration of gender differences in Adélie penguin foraging trip durations and diet at this location (described in Chapter 4) stimulated an investigation of the diving behaviour of these birds in relation to foraging trip duration and gender.

5.2 Materials and Methods

5.2.1 Study animals and deployment of dive recorders

Fieldwork was carried out at Béchervaise Island (67°35'S, 62°48'E) near Mawson station, Mac.Robertson Land, Antarctica during the austral summers of 1992-93 and 1993-94. The Adélie penguin population on this island consists of approximately 1800 breeding pairs and is the site of a long-term ecological monitoring program (Kerry *et al.* 1993). Dive records were obtained from seven male and four female penguins during January in 1992-93, and from four males and three females between late December and January in 1993-94 (Table 5.1). Deployment of dive recorders covered the guard and crèche stages of the Adélie penguin breeding cycle (Fig. 5.1).

Penguins chosen to carry dive recorders were breeding adults of known sex carrying implanted, individually unique electronic identification tags (Kerry *et al.* 1993; Clarke and Kerry 1994). Birds were captured at the nest as they prepared to depart, following return of their mates. Nests were observed at three-hourly intervals to determine the approximate times of departure and return of the birds, and checked daily to determine the status of eggs and chicks. Exact foraging trip durations were later calculated from data collected automatically by an electronic weighbridge and tag detector placed between the colony and the sea (Kerry *et al.* 1993).

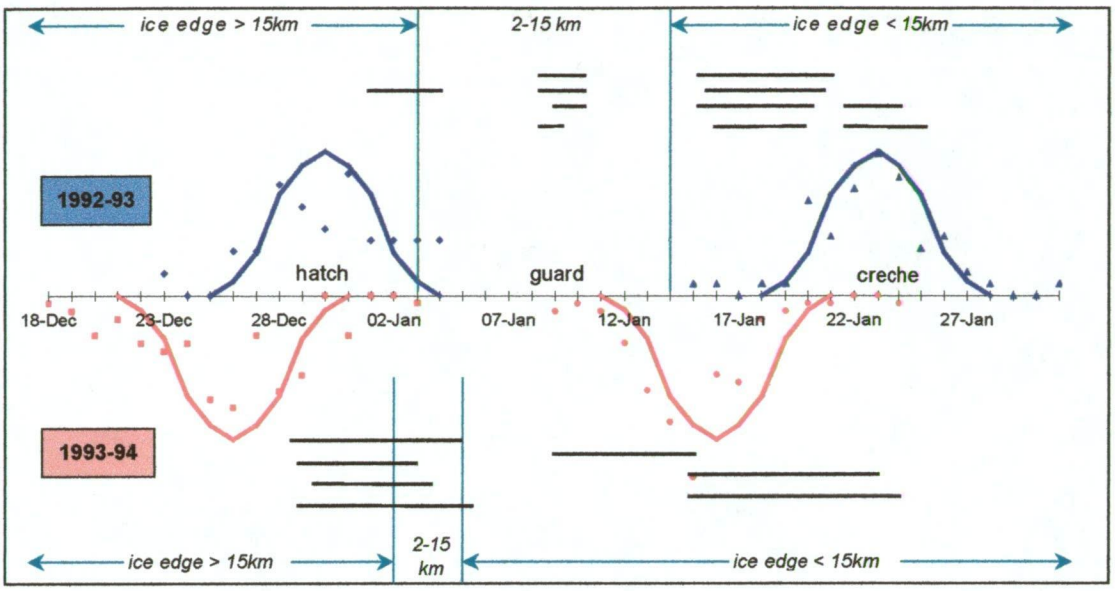

Figure 5.1.
Diagram showing deployments of TDRs (horizontal lines) in relation to the breeding cycle (curves of best fit through dates of hatch and entry into crèche for 100 observed nests) and the fast ice extent (vertical lines) over two seasons. The fast ice extent normally decreases gradually during the first half of January; the rapid break out in 1993-94 was unusual.

The electronic time-depth recorders (TDRs) used in this study were Mk 5 TDRs manufactured by Wildlife Computers (Woodinville, Washington) programmed to sample depth at 5 s intervals. Each device measured 65 x 35 x 15 mm and weighed 50 g. An immersion sensor was used to restrict data collection to periods when penguins were actually swimming; durations of "dry" periods when birds were on land or ice were timed. Each penguin was weighed prior to attachment of the TDR which was glued onto the feathers of the lower back using rapid-hardening epoxy glue (Loctite 401™) and secured in place with cable ties threaded under the feathers and around the device. Birds were returned to their nests where they remained for periods of up to 48 hours before departing to sea.

Individual birds carried recorders for one to four consecutive foraging trips during each deployment (Table 5.1). Penguins returning from their final trips were captured before feeding their chicks, and their stomach contents collected by water off-loading (Wilson

1984). Dietary components were sorted by mass into the categories of *E. superba, E. crystallorophias*, unidentified krill, fish, squid and amphipods.

Extent of fast ice from the colony was noted at the time of each trip and categorised as: >15 km, 2-15 km or <2 km (Table 5.1, Fig. 5.1). The changing distance between the colony and the fast-ice edge throughout both breeding seasons was recorded using satellite images of the region supplemented by visual observations from the highest point of the island (50 m ASL).

5.2.2 Dive analysis and statistical methodology

Software packages provided by Wildlife Computers were used to examine and analyse the dive records. Strip charts were produced to provide a general overview of each trip; following this all dives were individually viewed and categorised as either foraging or travelling dives. Dives shallower than 3 m were excluded from analyses as wave action and instability in the zero offset of the devices prevented accurate discrimination of individual shallow dives. The dive software stored the date, start time, maximal depth, duration, bottom time, descent and ascent rates of each dive, along with the classification category chosen by the analyst.

Classification of dives into the two classes of foraging dives and travelling dives was carried out according to the method described in Chappell *et al.* (1993a). Foraging dives were designated as those with maximal depths >20 m or durations >1.0 min, while dives with durations <20 sec were classified as travelling dives. The remaining dives (with durations between 20 sec and 1.0 min) were categorised as foraging dives if they showed abrupt inflections in ascent and descent rate, and as travelling dives if they lacked such inflections (Fig. 5.2). The software defined bottom time as the duration spent at or below 85% of maximal dive depth. Frequency distributions of dive durations, maximal depths and percent bottom time were derived for each foraging trip, and for successive trips made by individual birds.

Individual foraging trips were designated as long (>40 hr) or short (<40 hr) on the basis of the research described in Chapter 4 which demonstrated over four seasons a consistently bimodal distribution of overall colony foraging trip durations with modal values between 15-25 and 45-65 hr. Foraging trips were further grouped by gender within the long and short duration categories. Dive characteristics of the four gender-duration groups were compared using analysis of variance (ANOVA). Diurnal patterns in dive frequencies for each hour of the day were similarly investigated.

Individual penguins were considered as the primary units supplying data for comparison between genders and trip duration categories. Comparisons were thus made between three females and six males carrying out short trips, and four females and five males carrying out long trips (Table 5.1). Multiple trips undertaken by individual birds were pooled for the ANOVA providing they were all of either short or long duration. Three penguins carried out trips of both short and long duration (Table 5.1). In these cases only the data from their long trips were used in the ANOVA. The short trips made by these three birds were, however, not ignored, being used in comparison with their long trips to provide a basis, free of bird-to-bird variation, for examining differences between long and short trips. Paired t-tests were used for this latter comparison.

Comparisons of mean dive depth, duration and percent bottom time among groups of penguins in the different trip duration and gender categories were made using ANOVA with a factorial arrangement (SPSS statistical software). Levene's homogeneity test for equality of variances was employed to compare the variability of groups. Where there was evidence of differences among groups, pair-wise comparisons of means were carried out based on the predicted least significant difference procedure. The range was adopted for the purpose of graphically presenting differences in the variability of mean values because it was considered more meaningful from the viewpoint of interpretation.

Logistic regression analysis using a stepwise method was employed to identify predictor variables to allow discrimination between long and short trips and between males and

females in terms of dive characteristics. Potential predictors included ranges and mean values of dive depth, dive duration and percent bottom time.

Within group correlations between dive characteristics were computed using the Pearson-product-moment correlation coefficient. Computations were carried out using the residuals obtained in the application of the design model in order to remove the systematic effects of trip duration and gender (SPSS statistical software).

5.3 RESULTS

5.3.1 Dive depths and durations

Altogether, 18 individual birds carrying TDRs carried out 34 foraging trips over two breeding seasons. Mean and maximal dive depths and durations, and mean percent bottom time for each trip are detailed in Table 5.1. Dive records were obtained from 25 trips during the guard period and 9 trips during the crèche period. Foraging trip durations ranged from 8-110 hr with a mean of 41 ± 31 hr (mean ± SD). Between 40 and 100% of each trip was spent in the water. The majority (77%) of long trips in this study were greater than 60 hr in duration, while 90% of short trips lasted less than 30 hr (Table 5.1).

A total of 29 817 dives to depths of >3 m was analysed. Sixty-six percent of these were classed as foraging dives. The depth of all dives was 18.5 ± 0.12 m (mean ± SEM, range 3-112 m) and the depth of the 19 689 dives classed as foraging dives was 26.2 ± 0.14 m (mean ± SEM, range 3-112 m). The duration of all dives was 1.02 ± 0.004 min (mean ± SEM, range 0.08-3.92 min) and that of foraging dives was 1.30 ± 0.004 min (mean ± SEM, range 0.33-3.92 min). Percent bottom time was 26.4 ± 0.11% (mean ± SEM, range 0-95.4%) for all dives and 31.0 ± 0.12% (mean ± SEM, range 0-95.4%) for foraging dives only. Maximal dive depths for individual trips ranged from 14 to 112 m.

Table 5.1 Details of foraging trips of 18 individual Adélie penguins over two seasons grouped by trip duration, gender and ice extent, and showing mean dive statistics for each trip. Year 1 is the 1992-93 season and year 2 is 1993-94. Short trips (S) were of <40 hr duration and long trips (L) >40 hr. Prey types are designated: A = amphipods, S = *E. superba*, C = *E. crystallorophias*, F = fish, K = unidentified krill. Ratios of prey types within a stomach sample are indicated.

Bird ID	Breed Stage	Sex	Long or Short Trip	Fast Ice Extent (km)	Year	Trip Duration (hr)	Diving time (hr)	No. of Dives	% dives classed "foraging"	Max Dive Depth (m)	Mean Dive Depth (m)	sd	Max Dive Duration (min)	Mean Dive Duration (min)	sd	Mean % Bottom Time	sd	Meal Mass (g)	Ratio of Prey Types (by mass)
G*	guard	f	L	2-15	2	43	33	1169	68	84	18.51	20.46	2.67	0.95	0.55	27.07	18.40	374	*S*:F (2:1)
B*	guard	f	L	<2	1	85	67	2679	72	110	19.29	21.29	2.83	1.05	0.57	30.03	17.68		
H	creche	f	L	<2	1	69	47	1936	49	73	16.48	18.93	3.33	0.83	0.64	23.69	18.90	174	*S*:F (2:1)
Q	creche	f	L	<2	2	64	55	2003	58	78	17.06	18.76	3.33	1.08	0.56	27.97	16.26		
Q	creche	f	L	<2	2	90	71	2494	67	93	17.93	18.35	3.17	1.15	0.54	30.57	17.11	436	*S* (100%)
N	guard	m	L	<2	1	110	70	2591	67	73	17.79	16.61	2.83	0.99	0.56	29.04	18.87		
R	guard	m	L	<2	2	47	26	725	74	81	24.71	22.48	2.75	1.34	0.70	28.48	16.48		
R	guard	m	L	<2	2	63	26	898	70	63	11.87	13.43	3.50	0.96	0.56	25.05	20.96		
F*	creche	m	L	<2	1	58	49	1936	72	93	21.29	23.30	3.83	1.06	0.68	26.22	18.13		
F*	creche	m	L	<2	1	78	53	1969	61	88	17.29	20.61	3.00	0.93	0.64	25.50	18.49	376	*S* (100%)
K	creche	m	L	<2	2	67	43	1295	72	76	21.96	18.68	3.08	1.23	0.65	30.04	15.07		
K	creche	m	L	<2	2	94	55	1502	90	91	29.41	22.04	3.58	1.38	0.64	30.37	16.11	396	*S*:F (5:1)
O	creche	m	L	<2	1	110	81	2755	64	106	19.75	23.36	3.08	1.06	0.72	28.93	21.62	501	K:F (9:1)
G*	guard	f	S	>15	2	39	19	366	63	57	13.76	12.47	3.33	0.85	0.61	18.69	18.55		
G*	guard	f	S	>15	2	29	8	498	72	48	16.13	10.46	1.83	0.83	0.44	18.72	16.32		
P	guard	f	S	>15	2	21	7	228	79	30	11.93	6.34	2.58	1.11	0.54	22.91	18.78		
P	guard	f	S	>15	2	20	8	350	79	32	16.03	6.31	1.83	0.93	0.35	24.39	17.01		
E	guard	f	S	2-15	1	17	2	87	23	30	4.82	4.52	2.33	0.36	0.43	13.54	20.69	152	A (100%)
P	guard	f	S	2-15	2	23	14	537	76	76	17.06	14.06	2.42	1.06	0.50	26.82	18.99	172	*S* (100%)
B*	guard	f	S	<2	1	12	1	32	69	10	5.06	2.06	1.08	0.40	0.28	23.92	26.54		
I	creche	f	S	<2	1	29	20	856	55	86	10.03	15.97	2.83	0.68	0.59	19.67	21.87	134	*C* (100%)
C	guard	m	S	>15	2	22	7	298	33	24	6.01	4.73	3.92	0.40	0.39	13.01	20.70		
C	guard	m	S	>15	2	13	2	69	38	14	4.35	2.03	3.50	0.44	0.46	15.54	22.32		
C	guard	m	S	>15	2	17	2	94	35	22	4.99	4.23	1.42	0.42	0.34	19.60	28.13		
J	guard	m	S	>15	2	15	4	159	45	18	5.74	3.14	1.33	0.48	0.33	13.97	20.61		
J	guard	m	S	>15	2	15	6	237	54	18	5.92	2.70	1.92	0.49	0.29	16.28	21.60		
L	guard	m	S	>15	1	35	13	307	75	112	40.88	35.27	3.17	1.46	0.79	19.30	16.67	38	A (100%)
A	guard	m	S	2-15	1	19	12	388	83	54	25.21	13.79	2.33	1.26	0.61	23.25	14.83	300	F:A (1:1)
C	guard	m	S	2-15	2	13	8	216	66	80	19.03	18.95	2.33	0.92	0.63	20.90	19.94	97	*S*:F (2:1)
D	guard	m	S	2-15	1	8	5	161	81	51	25.19	13.15	2.42	1.19	0.53	18.47	12.69	113	F (100%)
J	guard	m	S	2-15	2	15	7	249	75	64	26.80	15.11	2.00	1.05	0.47	19.31	13.50		
J	guard	m	S	2-15	2	21	7	289	68	59	17.17	12.91	1.75	0.83	0.44	16.62	16.52	73	*S*:F (1:1)
M	guard	m	S	2-15	1	12	7	294	44	67	7.03	10.40	2.08	0.49	0.43	13.81	21.13	213	F:A (6:1)
F*	guard	m	S	<2	1	10	5	150	66	52	20.53	15.62	1.92	0.86	0.53	17.52	15.73		

* Individual birds that made both long and short trips.

Twenty-seven percent of all dives were to depths <5 m; 54% were <10 m; 68% <20 m and only 11% >50 m. Many of the dives to depths greater than 20 m occurred during periods of repetitive diving to similar depths (Fig. 5.2a). Shallower dives (<15 m), however, tended to show a less regular pattern with little clear-cut visual distinction between foraging and travelling dives (Fig. 5.2b). The majority (58%) of dives that were classified as non-foraging (and thus assumed to be travelling) were less than 5m in depth.

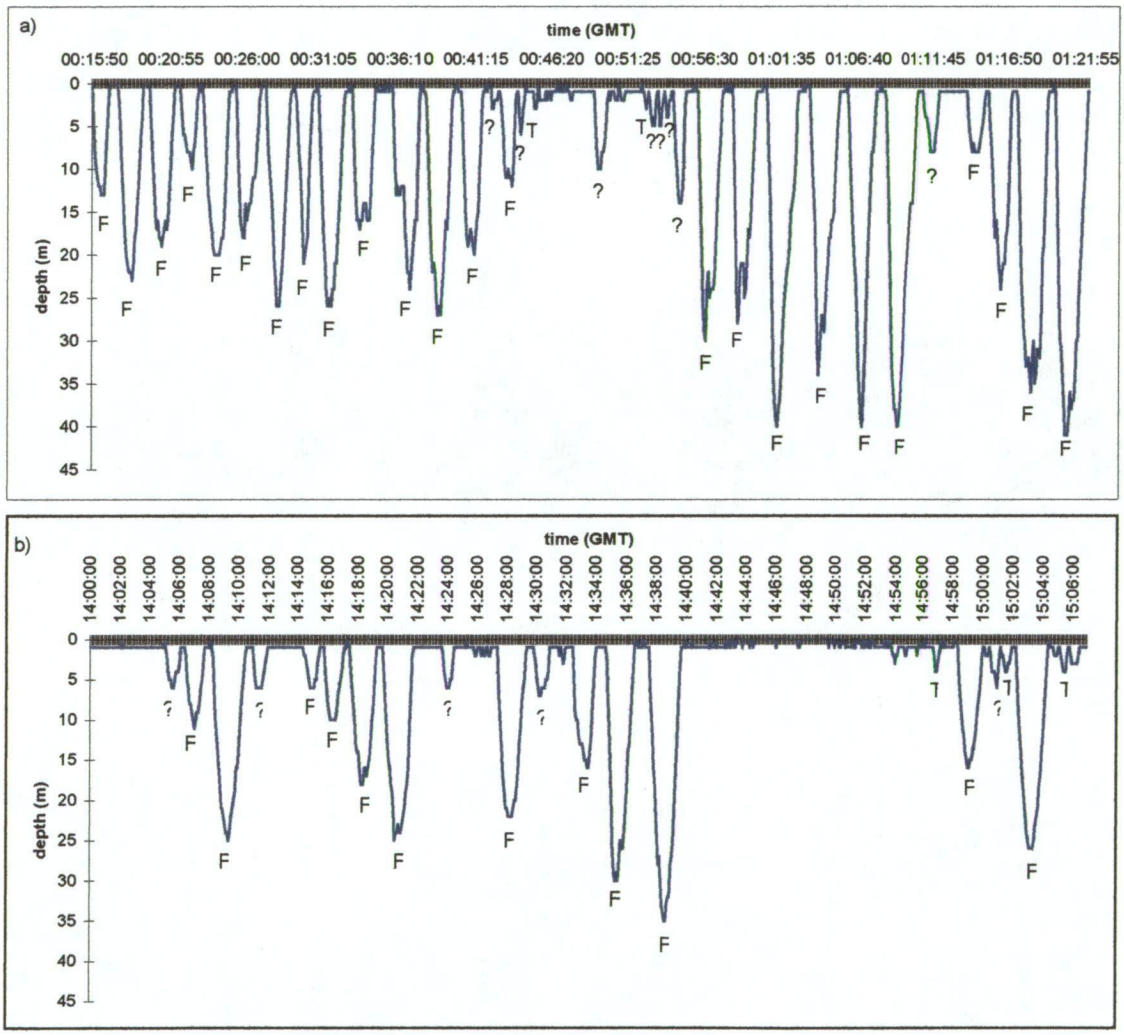

Figure 5.2.
Sections of individual dive profiles showing foraging dives (F), travelling dives (T) and dives subjectively classified as foraging or travelling on the basis of profile shape (?). Dives of <3 m were difficult to distinguish from background noise and thus not analysed. a) Start of a period of diving from the middle of a foraging trip; b) dives performed by a penguin within an hour of entering the water at the start of a foraging trip. Local time is GMT+4 hr.

Shallow dives (<10 m) were greatest in frequency during all trips. Frequency distributions for the subset of dives classified as foraging were essentially the same as those for all dives apart from a reduction in the proportion of dives in the lowest depth and duration categories. Due to the difficulty in distinguishing between shallow foraging and travelling dives (illustrated in Fig. 5.2b) all the following analyses were carried out using the complete set of dives.

Table 5.2. Mean maximal dive depth, duration and percent bottom time for groups of birds based on a) trip duration, b) gender, and c) gender and duration. Standard deviations are shown in brackets.

	Trip Duration/ Gender Group	Maximal dive depth (m)	Dive duration (min)	% bottom time	% dives between 6:00 and 18:00	N birds
a)	Short trips	17.1 (11.5)	0.86 (0.38)	18.5 (3.9)	54.3 (23.3)	9
	Long trips	19.1 (2.8)	1.05 (0.13)	27.9 *** (2.2)	51.7 (8.4)	9
b)	Males	20.3 (9.1)	1.02 (0.31)	22.6 (5.8)	51.5 (21.3)	11
	Females	14.6 (5.3)	0.86 (0.27)	24.1 (5.8)	55.4 (7.5)	7
c)	Short trip males	20.5 (12.5) *	0.95 (0.40) **	18.1 (3.2)	54.3 (28.3) ***	6
	Short trip females	10.2 ** (5.4)	0.69 * (0.33)	19.5 (5.9)	54.3 (12.4)	3
	Long trip males	20.1 (3.4)	1.10 (0.13)	28.1 (1.8)	48.0 (9.9)	5
	Long trip females	18.0 (1.2)	0.99 (0.12)	27.6 (2.9)	56.3 (2.6)	4

Asterisks indicate values of mean or range that are significantly different from all others in that section (see text). Significance: * 5% level; ** 1% level; *** 0.1% level.

5.3.2 Dive characteristics related to foraging trip duration and gender

Combined statistics for the different gender and trip duration groups are shown in Table 5.2. Frequency distributions of dive depths, durations and bottom times were produced for each gender-duration group (Fig. 5.3) and for long and short trips of combined genders (Fig. 5.4).

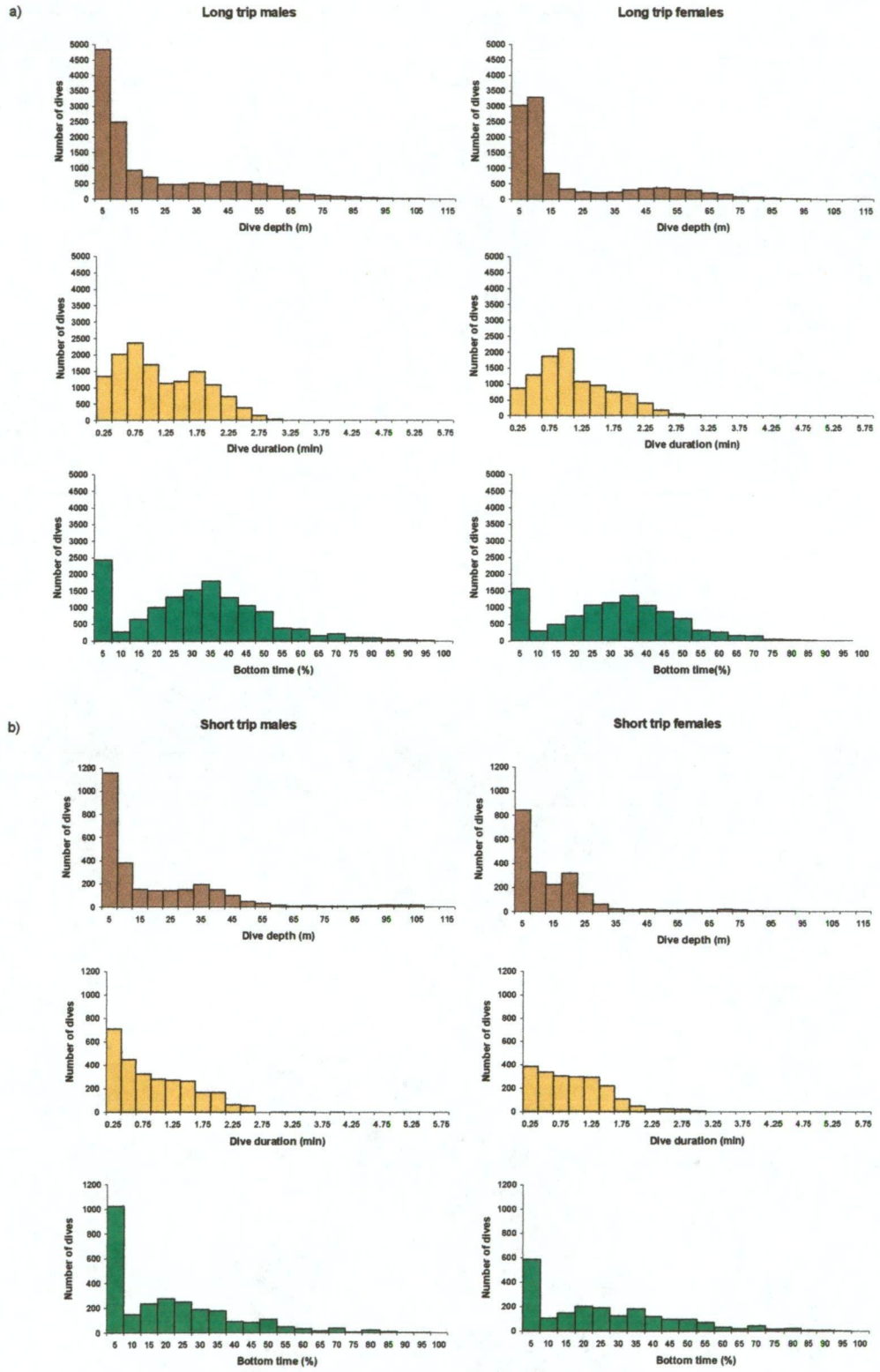

Figure 5.3.
Frequency distributions of maximal dive depths, durations and percent bottom time for all dives >3 m, grouped by gender and trip duration. Data are presented for males and females undertaking a) long trips and b) short trips.

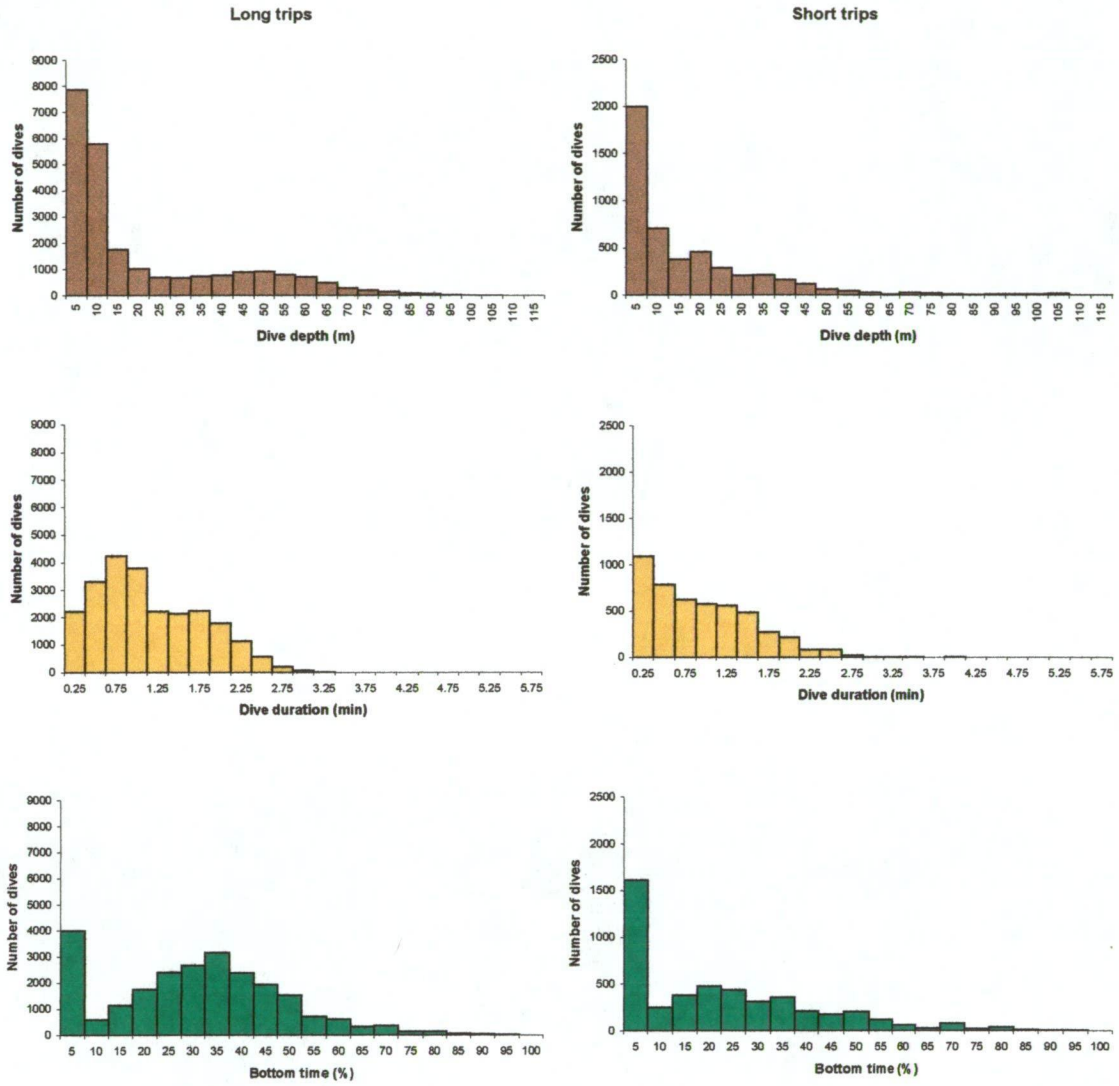

Figure 5.4.
Frequency distributions of maximal dive depths, durations and percent bottom time for long trips versus short trips (males and females combined).

5.3.2.1 Dive depth

Penguins making short trips (<40 hr) rarely dived deeper than 50 m, with 91% of all dives <40 m in depth (Figs 5.3&5.4). Most short trips took place during the guard stage when fast ice was present around the island. Long trips (>40 hr) occurred during both the guard and crèche stages, and showed a bimodal pattern of dive depths with the secondary peak occurring at 40-70 m (Figs 5.3&5.4).

Male birds undertaking short trips had a range of mean maximum dive depths that averaged approximately three times that of females on short trips or birds of either sex on long trips (p=0.02) (Table 5.2, Fig. 5.5a). The mean value for maximum dive depth of females making short trips (10.2 m) averaged only half the depth of birds of either gender making long trips, (20.1 and 18.0 m for males and females respectively, p=0.01) (Table 5.2, Fig. 5.5a). Although males on short trips averaged at 20.5 m twice the mean depth of females on short trips, the difference was not significant due to the greater variability associated with the males.

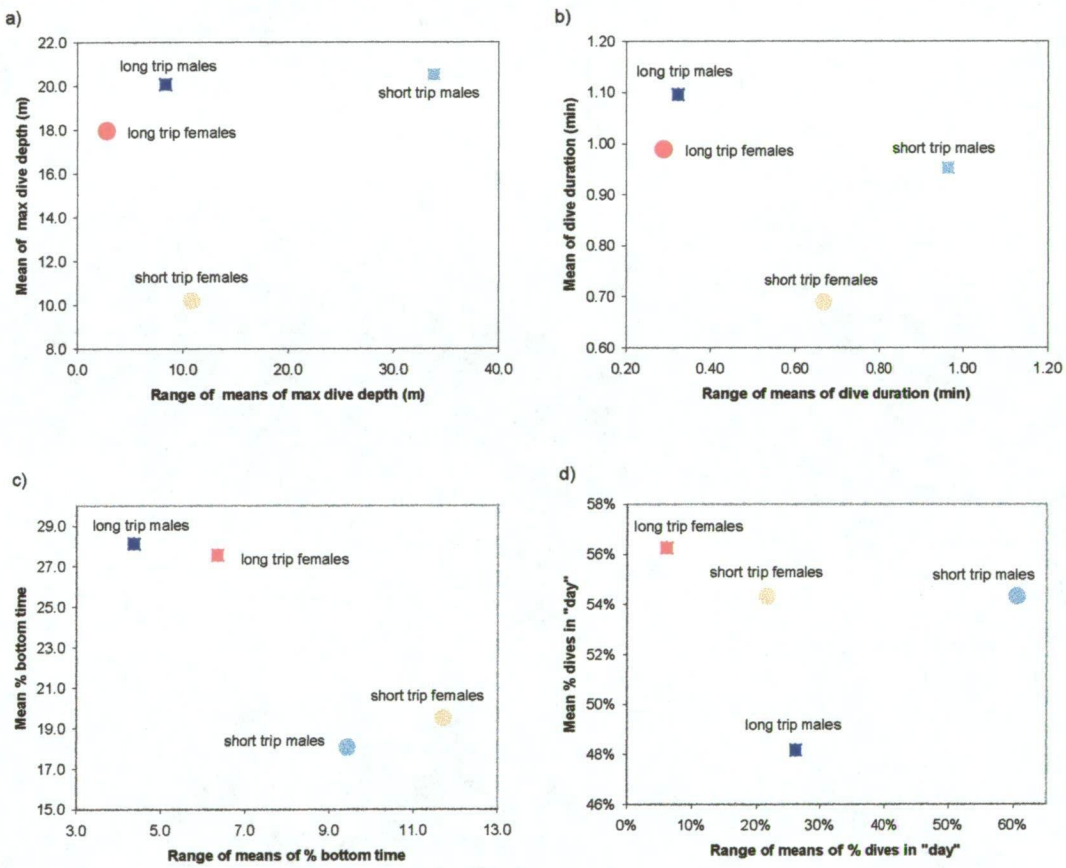

Figure 5.5.
Ranges and means of dive parameters for males and females carrying out long and short trips. a) maximal dive depth, b) dive duration, c) percent bottom time, d) percentage of dives occurring between 6:00 and 18:00 local time.

5.3.2.2 Dive duration

Male birds undertaking short trips showed greater variability in mean dive durations than the other three groups ($p=0.007$) (Table 5.2, Fig. 5.5b). Females on short trips made on average dives of shorter duration than did those of other groups, with a mean of 0.69 min. This duration was significantly different to that of males making long trips, which averaged 1.10 min ($p<0.05$) (Table 5.2, Fig. 5.5b).

5.3.2.3 Mean percentage of time on the bottom

Penguins of both sexes making long trips spent on average approximately fifty percent more time proportionally on the bottom than did those making short trips ($p<0.001$) (Table 5.2, Fig. 5.5c). The mean percent bottom time for birds on long trips was 27.9%, and for those on short trips, 18.5%. No significant gender differences in mean percent bottom time were found.

Logistic regression analysis identified percentage of time on the bottom as a strong indicator for discrimination between trips of long and short duration. Trips from sixteen of the eighteen birds could be correctly classified using a rule based on this variable alone. No other variable or combinations of variables could be used to discriminate between these two types of trip. Neither did logistic regression analysis identify any one predictor variable or combination of variables that could be used to discriminate between the trips of males and females.

5.3.2.4 Diurnal patterns

Frequencies of diving and dive depth for each hour of the day (local time) are shown in Figure 5.6 for each of the four groups defined by trip duration and gender. Times of day when the sun was below the horizon are also shown, although twilight remained present during these hours. Analysis of the differences in the percentages of dives taking place in the "day" (6:00 to 18:00) versus the "night" (18:00 to 6:00) showed no obvious diurnal patterns of diving frequency for any of the groups, consistent with the hypothesis of no diurnal variation (Table 5.2, Fig. 5.5d). However, male birds making short trips did have a range in percentage of dives occurring in the "day", which was more than four times the average of the other three groups ($p<0.001$). Further analysis

with "night" defined as 21:00 to 3:00 failed to detect any significant differences in diving frequencies between duration-gender groups.

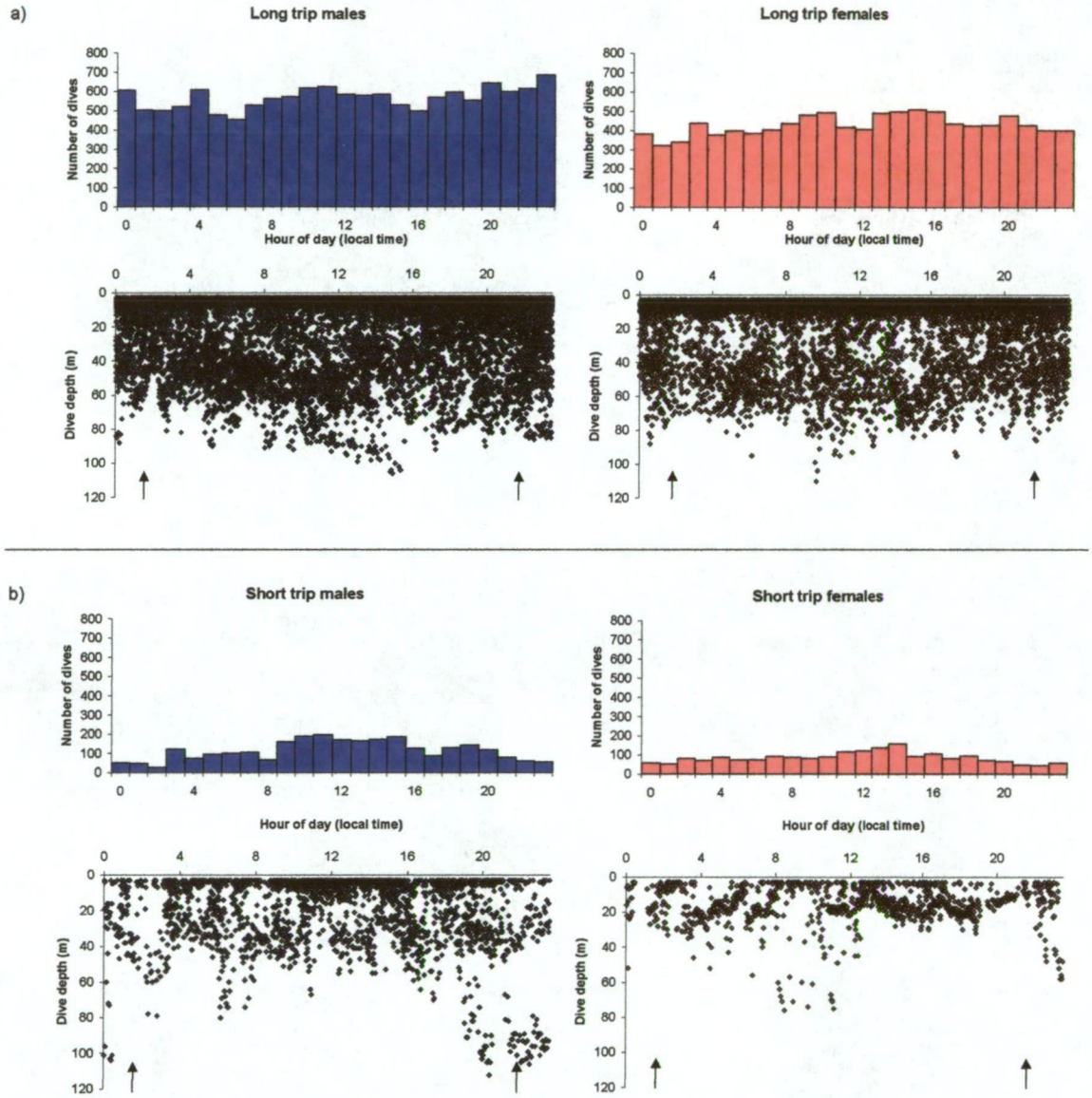

Figure 5.6.
Frequencies of diving and maximal dive depths during each hour of the day for males and females undertaking a) long trips and b) short trips. Arrows indicate the latest sunrise and earliest sunset times during the periods over which trips took place.

5.3.2.5 Birds making both long and short trips

Three birds, two females and one male, undertook trips of both long and short duration (Table 5.1). Paired comparisons of maximal dive depth, dive duration and percent bottom time showed that on their long trips these birds spent significantly more time on the bottom than on their short trips (p=0.01; Table 5.3). This finding was consistent with the between-penguin results reported above. No significant within-penguin differences were found for the other two variables examined (Table 5.3).

Table 5.3. Mean maximal dive depth, duration and percent bottom time for three individual birds that made trips of both long and short duration. Ranges are shown in brackets.

		Maximal dive depth (m)	Dive duration (min)	% bottom time	N dives
Long trips	Bird #3	19.3 (107)	1.05 (2.75)	30.0 (92.3)	2679
	Bird #8	19.3 (90)	1.00 (3.75)	25.9 (86.6)	3905
	Bird #9	18.5 (81)	0.95 (2.59)	27.1 (86.2)	1169
	Total	19.2	1.00	27.5 **	7753
Short trips	Bird #3	5.1 (7)	0.40 (1)	23.9 (76.9)	32
	Bird #8	20.5 (49)	0.86 (1.84)	17.5 (68)	150
	Bird #9	15.1 (54)	0.84 (3.25)	18.7 (93.2)	864
	Total	15.6	0.83	18.7 **	1046

** Significant differences between long and short trips (to the 1% level).

5.3.3 Correlations between dive parameters

Correlations between dive parameters are presented in Table 5.4. Dive duration was highly correlated with maximal dive depth (p<0.001). Percentage of time on the bottom was weakly correlated with dive depth (p=0.012) and somewhat more strongly correlated with dive duration (p<0.001). The percentage of dives occurring between

6:00 and 18:00 was negatively correlated with dive depth and duration (p=0.001 and p=0.002 respectively), but not correlated significantly with percentage of time on the bottom.

Table 5.4. Correlations between dive parameters based on residuals from the analysis of variance (see text).

	Maximal dive depth (m)	Dive duration (min)	bottom time (%)
Dive duration (min)	0.93 ***		
% bottom time	0.58 *	0.78 ***	
% dives between 6:00 and 18:00	-0.73 **	-0.69 **	-0.24

Asterisks indicate significant correlations. Significance: * 5% level; ** 1% level; *** 0.1% level.

5.3.4 Diet

In total, nine males and six females were stomach flushed on return from their trips during chick rearing (Table 5.1). Fish were present in the stomach contents of seven of the males but only in one of the female samples. All but one of the females on the other hand had eaten krill. Males showed a particular tendency to feed on fish on their short guard stage trips. These results are consistent with the sex differences in dietary preference described in Chapter 4.

Concurrent satellite-tracking studies indicated that birds that undertook long trips generally travelled to the edge of the continental shelf 80-100 km offshore to feed (Kerry *et al.* 1995a; Chapter 4). Stomach contents from six birds returning from long trips contained mainly krill (*E. superba*), with fish forming a minor component of the diet (Table 5.1).

5.3.5 Relationship between fast ice extent and diving behaviour

The fast ice gradually reduced from 15 to 2 km in northerly extent during 1992-93. In the following season strong winds broke up the fast ice and blew it out in only three

days (Jan 2-5); these corresponded with a single foraging trip of each of the four birds carrying depth recorders at the time (Fig. 5.1).

Most long trips during the guard stage occurred after the ice edge had receded to within 2 km of the colony and most short trips occurred while some ice was still present. Thus, mean dive depth, duration and percent bottom time all increased as the ice extent reduced (Tables 5.1&5.2). The birds, particularly males, showed a tendency to make shorter trips and perform shorter, shallower dives when fast ice was present than when there was open water. These results are again consistent with the sex differences in foraging behaviour described in Chapter 4 where male birds carried out more short trips in the guard stage than did females.

5.4 Discussion

5.4.1 Difficulties associated with classification of dives

Bimodal distributions of dive depths and durations have been demonstrated in studies of chinstrap (*Pygoscelis antarctica*), gentoo (*P. papua*) and rockhopper (*Eudyptes chrysocome*) penguin diving behaviour (Williams *et al.* 1992a&b; Bengtson *et al.* 1993; Wilson *et al.* 1997). These two types of dive profile have been assumed to represent travelling versus foraging dives. Studies of Adélie penguin diving behaviour have resulted in less distinct differentiation between profile types. Chappell *et al.* (1993a) reported dive distributions with a single mode but a variety of recognisable types of dive profile, while Naito *et al.* (1990) and Watanuki *et al.* (1993) found it difficult to differentiate between foraging and non-foraging dives on the basis of dive profile or depth distribution curves. The latter studies were carried out in regions of persistent fast ice where penguins forage under the ice and dive less deeply than do those in regions of open water (Watanuki *et al.* 1993, 1997).

The classification of dives as either travelling or foraging in this study proved difficult due to the lack of objective criteria to distinguish between foraging and travelling dives. Dives were classified according to the method of Chappell *et al.* (1993a) in order to make comparisons between results obtained from two different localities, the Antarctic Peninsula and East Antarctica. Many of the dives analysed by Chappell *et al.* (1993a) occurred in discrete bouts of repeated diving to similar depths which may have assisted in their differentiation of travelling, searching and hunting dives. In this study, however, many shallow dives of durations between 20 sec and 1.0 min were apparently randomly interspersed between deeper foraging and shorter travelling dives (Fig. 5.2b), and were thus difficult to classify as belonging to one or the other category. The statistical analyses were therefore carried out on the whole data set (with resultant loss of statistical power) rather than to risk introduction of artificial bias due to uncertainties in dive classification.

Only 46% of dives >3 m deep made by Adélie penguins at Torgersen Island (64°46'S, 64°05'W) on the Antarctic Peninsula were categorised as foraging dives by Chappell *et al.* (1993a), while 66% of dives in this study were classified as foraging using similar criteria. This difference suggests that the penguins at Béchervaise Island make more short shallow foraging dives than do those at Torgersen Island. However, the discrepancy could also be due to a different interpretation of "abrupt inflections in ascent or descent rate" when categorising dives of between 20 sec and 1.0 min in duration and <20 m in depth. The fact that movements of penguins in a three-dimensional space can only be recorded in two-dimensions by dive recorders adds to the difficulty in interpretation of dive profiles.

The sampling frequency at which depth data are obtained can also affect the appearance of a dive profile and will even alter the depth and duration statistics of a whole data set if the interval between readings is too large (Boyd 1993; Wilson *et al.* 1995). All TDRs in this study sampled at 5 sec intervals. Chappell *et al.* (1993a) used the same sampling interval in addition to some settings of 1 sec. At the latter resolution it would be expected that more, rather than fewer, dives would be considered to show "abrupt

inflections" in their profiles; thus the difference in results between the two studies is unlikely to be due to variation in sampling frequencies.

The Adélie penguins at Béchervaise Island have been shown to forage at a wide range of distances from the colony, ranging from as close as 5 km to as distant as the continental shelf break 120 km away (Kerry *et al.* 1995a, 1997; Chapter 4). Analyses of TDR records obtained from birds at this breeding locality have so far failed to provide an objective means of determining at which stage(s) on their journeys the birds are actually feeding as opposed to travelling and/or searching. Further, no studies of Adélie penguin diving behaviour to date have been able to definitively relate particular dive profiles to prey ingestion. The use of stomach temperature recorders in Adélie penguins (Wilson *et al.* 1993) and king penguins (Pütz 1994) has provided good associations between feeding intensity and dive bouts. However, only in African penguins (*Spheniscus demersus*) have direct correlations been made between prey ingestion events and individual dive profiles (Wilson *et al.* 1992; Wilson and Wilson 1995).

Further research is required to definitively differentiate foraging from non-foraging dives made by Adélie penguins from colonies in the Mawson region. The development of miniaturised cameras or beak-opening detectors that can be carried by penguins may enhance our detailed understanding of the diving behaviour of these birds in future years.

5.4.2 Diving in relation to trip duration and gender

The extensive foraging range of Adélie penguins in the Mawson region during chick rearing enables birds to forage in three distinct oceanographic zones each dominated by different micronekton communities. These zones include the area over the continental shelf (neritic community), the continental slope zone (krill dominated community) and the offshore oceanic zone (oceanic community) (Hosie and Cochran 1994). Birds from Béchervaise Island forage mostly in the krill-dominated and neritic zones (Kerry *et al.* 1994), but predominantly in only one on any given foraging trip.

Satellite tracking studies have shown that birds undertaking foraging trips of longer than 40 hr in duration usually travel 80-120 km to the continental shelf edge to feed (Kerry *et al.* 1995a; Chapter 4). Birds in the present study spent proportionally more time at the bottom of their dives on long trips than on short. One interpretation of this finding is that they were foraging intensively on small prey for much of the time they spent diving on these longer trips. The increased percentage of bottom time suggests that birds were carrying out a higher proportion of U-shaped dives on long trips. U-shaped dive profiles have been associated with prey ingestion in gentoo and African penguins (Wilson *et al.* 1996; Wilson and Wilson 1995).

Most birds from Béchervaise Island ingested larger quantities of krill (*E. superba*) on long trips than short, consistent with observations that the greatest krill concentrations are located further than 80 km from the colony (Kerry *et al.* 1997). Consumption of fish (particularly *Trematomus newnesi*, unpublished data) was, on the other hand, more common on short trips. The reduced proportion of bottom time on dives during short trips could be related to prey size, with fewer relatively large nototheniid fish being captured per dive compared to the prey ingestion rate for penguins pursuing krill.

The majority of short trips in this study took place during the guard stage when some degree of fast ice was present. Satellite tracks from two individuals that carried satellite trackers as well as dive recorders showed that these birds were foraging in the neritic zone, within 15 km of the colony. This foraging range was consistent with that described in Chapter 4 for birds undertaking short trips. Females foraged at shallower depths than males on long trips, while males showed greater variability in dive depth and duration than did females. Birds brought back a variety of prey organisms from their short trips, including fish, amphipods and *E. crystallorophias* as well as small quantities of *E. superba*.

Qualitative examination of dive depth frequency histograms from individual male birds carrying out short trips demonstrated a wide range of depth profiles (consistent with the

range of mean depths exhibited in the statistical analysis). Some males restricted the majority of their diving activity to the top 10 m of the water column, while others performed repeated dives to depths between 20 and 45 m. Stomach samples from three birds in the latter group contained fish, and identification of nototheniid otoliths suggested that these birds were likely to be feeding on benthopelagic prey. Birds performing only shallow dives (<10 m) foraged when the sun was above the horizon, suggesting that they may have been feeding under the ice where ambient light levels were too low for successful prey capture at night.

The variety of dive profiles obtained from birds carrying out short trips in the neritic zone reflects the diversity of prey species captured in this coastal region. Further directed research with greater sample sizes is required to effectively correlate dive characteristics to feeding events, prey types and gender of birds foraging in this region.

5.4.3 Diurnal variation in diving behaviour

Obvious diurnal patterns of diving frequencies and depths recorded for various penguin species have been linked to day length and light intensity (Wilson *et al.* 1989a, 1993, 1997) or diel migration of krill (Croxall *et al.* 1988; Williams *et al.* 1992a; Bengtson *et al.* 1993; Croll *et al.* 1993). Although some studies of Adélie penguin diving behaviour at latitudes lower than 65°S have found distinct diurnal patterns in both dive depths and frequencies (Wilson *et al.* 1993), others have found little diurnal variation in dive depth despite diurnal patterns of frequency (Naito *et al.* 1990; Chappell *et al.* 1993a; Watanuki *et al.* 1993). These differences indicate that prey distribution may exhibit greater diel fluctuations at some locations than at others, as has been postulated by Miller and Hampton (1989).

No distinct diurnal patterns in diving frequencies or maximal dive depths were apparent on long trips in this study. Ambient light levels during December and January at the latitudes where the penguins from Béchervaise Island forage (66-68°S) appear to be sufficient for prey to be pursued throughout the whole 24 hr period. In addition, there is

evidence that krill offshore from the Mawson coast undergo only weak vertical dial migration, if any, during summer months (Nicol, pers. com.), unlike that described for krill populations around South Georgia and parts of the Antarctic Peninsula (Croxall *et al.* 1988; Croll *et al.* 1993).

Diurnal dive patterns observed at latitudes higher than 65°S may be related to the formation of surface ice during the night and early morning, which prevents access by penguins to the water, rather than to light intensity as such (Watanuki *et al.* 1997). At Béchervaise Island (67°35'S) the presence of sea ice until early January dampens wave movements and allows ice to form on the surface of the water in inshore regions during the night. By late January wave movement and katabatic winds prevent overnight surface ice formation. The greatest diurnal variation in dive frequencies was detected on short trips when fast ice was present. These patterns are likely to be related more to surface ice formation and reduced light intensity from pack ice cover than to changes in day length per se.

The lack of distinct diurnal patterns in Adélie penguin foraging behaviour at Béchervaise Island has been demonstrated in other studies at this location. The arrival and departure times of birds to and from the colony over the whole breeding season have been automatically monitored (Kerry *et al.* 1993) and, in contrast to Wilson *et al.* (1989a), no distinct diurnal pattern in their return times to the colony from foraging trips has been detected (Kerry and Clarke, unpublished data). Positional fixes from foraging birds carrying satellite trackers also show no diurnal patterns of submergence (Kerry *et al.* 1995a).

5.4.4 Diving in relation to fast ice extent

In general, Adélie penguins foraging in open water tend to dive to greater depths than do those feeding under fast ice. Maximal depths reached by penguins feeding in ice-free waters in Prydz Bay ranged between 79 and 175 m (Whitehead 1989), and at Esperanza

Bay on the Antarctic Peninsula 5% of underwater time was spent deeper than 50 m (Wilson *et al.* 1989a).

At Torgersen Island on the Antarctic Peninsula the mean maximal depth of foraging dives by Adélie penguins was 26 m (Chappell *et al.* 1993a). This average depth is similar to the deepest dive (27 m) recorded by Naito *et al.* (1990) for penguins feeding near Syowa station (69°00'S, 39°35'E) in East Antarctica where fast ice persists throughout the summer. Adélie penguins foraging for 2-3 week old chicks near Syowa dived almost exclusively to depths of less than 20 m with mean maximal dive depths ranging between 6.1 and 10.9 m. Chick survival indicated that the birds were successfully capturing prey at these shallow depths, and the researchers were unable to differentiate between travelling, searching and feeding dives. All dives were believed to be foraging dives since the presence of fast ice around the foraging sites forced the birds to travel by walking. Krill were apparently available in the shallow coastal waters immediately beneath the sea ice. Watanuki *et al.* (1993) studied the diving behaviour of Adélie penguins in Lutzow-Holm Bay, 25 km from Syowa with similar findings.

Adélie penguins from Béchervaise Island feeding small chicks frequently restrict their foraging to local waters, catching amphipods, fish and *E. crystallorophias*. Dives at this stage tend to be shallower than later in the season, and it is possible that some prey are being captured directly underneath the fast ice. During the crèche stage, when the ice is at its minimal extent, birds tend to travel greater distances and dive longer and deeper. It appears that as the sea ice disperses local food supplies become scarce or more sparsely distributed, and breeding birds need to travel further from the colony to find sufficient food to support their growing chicks.

Few studies have been able to definitively relate penguin diving depths to prey distributions (Croll *et al.* 1993). Many, however, have inferred that this is indeed the case (Lishman and Croxall 1983; Whitehead 1989; Wilson 1989a; Naito *et al.* 1990; Wilson *et al.* 1991, 1996; Williams *et al.* 1992a; Bengtson *et al.* 1993; Croxall *et al.* 1993; Watanuki *et al.* 1993; Tremblay *et al.* 1997). It is likely that the presence of sea

ice affects the spatial and temporal distributions of prey (O'Brien 1987; Naganobu and Kawaguchi 1993) and that the diving behaviour of penguins will reflect these changes.

The Adélie penguins at Béchervaise Island dive to a wide range of depths and appear to forage successfully at shallow depths in areas of heavy ice as well as more deeply in regions of open water. Satellite tracking in combination with depth recorders and dietary studies has shown that the birds feed at a variety of locations on a correspondingly varied group of prey organisms (Kerry *et al.* 1994; Chapter 4). Several factors including the wide foraging range of birds at this colony, the variations in prey species taken, the patchy and generally low abundance of krill in the region (Hosie *et al.* 1988), and the catastrophic loss due to starvation of all chicks in the local region during the 1994-95 season (Kerry *et al.* 1995b) combine to suggest that food is not always readily available at this location. It would seem probable that the variations in diving behaviour found among and within individuals, and the changes that occur as environmental conditions alter, reflect the capacity of Adélie penguins to modify their foraging strategies in response to spatial and temporal variations in the distribution of their prey. Further research directed specifically at the relationships between penguins and their prey is required to attain a more accurate understanding of the foraging behaviour of this species in the Mawson region.

CHAPTER 6: GENERAL DISCUSSION

The preceding chapters describe a multi-year investigation into the foraging strategies and diving behaviour of Adélie penguins at Béchervaise Island, East Antarctica, in relation to gender, environmental conditions and breeding success. Some of the technologies used to provide data for this study, namely the APMS and various deployable instruments, have also been described and evaluated in detail. This final chapter comprises a summary of findings in regard to the use of implanted transponders in penguins, a discussion of foraging strategies of Adélie penguins as evidenced by gender differences and diving behaviour and a brief appraisal of the relevance of this work to programmes engaged in the long term monitoring of Adélie penguins.

6.1 IMPLANTED TRANSPONDERS

The use of implanted transponders has proved to be a valuable means of acquiring large quantities of data on penguin foraging trip durations as well as enabling automatic detection of inter-annual survival of adults and chicks. These data have allowed statistically significant sex differences in foraging behaviour to be demonstrated and are now beginning to provide a comprehensive picture of colony demography and fledgling survival rates. Implanted transponders are a reliable means of long-term marking for penguins providing they are injected carefully at sites where migration is least likely to cause harm. They have advantages over flipper bands, which carry an energetic cost to the birds wearing them (Culik *et al.* 1993) and also have a tendency to open and become lost over time. The lower return rate of banded *versus* tagged adults observed over the 1995 winter at Béchervaise Island may have been related to persistence of the preceding breeding season's poor food availability into winter, affecting most severely those birds that carried the additional energetically costly burden of a flipper band.

6.2 FORAGING STRATEGIES

Studies prior to the onset of the research described in this thesis had shown that Adélie penguins rearing chicks at Béchervaise Island carried out both short and long foraging trips, with shorter trips tending to occur most when chicks were small and longer trips once the chicks were left unguarded. Birds making short trips foraged within the neritic zone, returning with amphipods, *E. crystallorophias* or *P. antarcticum* while those making longer journeys travelled 80-120 km to the shelf break and returned with predominantly *E. superba*. These patterns were further investigated in the work described in Chapter 4 to show that much of the observed variation in trip duration could be related to sex differences in foraging behaviour. Female penguins made on average longer foraging trips than males, ranged greater distances more frequently and consumed larger quantities of *E. superba* compared to males which made shorter journeys to closer foraging grounds during the guard period and fed more extensively on fish throughout chick rearing.

Variations in foraging strategies were further analysed in relation to diving behaviour in the study described in Chapter 5 to show that penguins foraging close to the colony dived to shallower depths, on average, than those foraging at the shelf break. Further, it became apparent that diving behaviour even within the neritic zone showed marked variability in depth profiles and diurnal patterns. Some of this variability could be related to fast ice extent and diet; sex differences were also apparent.

The sex differences in foraging behaviour described in Chapters 4 and 5 are likely to result from the combined effects of several factors. Firstly, the energy budget required for reproduction (reproductive effort) in Adélie penguins has been shown to differ between the sexes during various stages of the breeding cycle. Chappell *et al.* (1993b) found that male Adélie penguins put more of their reproductive effort into courtship and incubation than did their mates while female birds expended more energy during the chick rearing period than did the males. The observations described in Chapter 4 that

males feed closer to the colony during the guard stage than do females while females spend longer at sea and forage further afield are consistent with this finding.

Intraspecific partitioning of foraging activities is a second factor that may help explain the sex differences observed in this study. Males tend to forage close to the colony feeding on fish, while females frequently travel greater distances to the shelf break to capture krill. Sex differences in dietary preference may become particularly important when food supplies are short as a means of both reducing intraspecific competition and of maximising the chances of one member of the pair locating food for the chicks without excessive waste of overall search effort. When local food supplies are apparently abundant males are able to provide meals of similar (sometimes greater) size for their chicks than can females that travel further afield. However, the shelf edge is normally a predictable region of food supplies (particularly krill), while local prey availability may vary. Females may choose to travel these longer distances in the early stages of chick rearing in order to exploit a more reliable food resource.

Analysis of weight data from the APMS has provided further insights into possible mechanisms underlying the observed two-fold foraging strategy of Adélie penguins in the Mawson region. In contrast to the results of Chappell *et al.* (1993b) male penguins at Béchervaise Island were found to be sufficiently heavy at the time chicks hatched to be able to afford to lose body condition whilst provisioning their young offspring. Females on the other hand could less afford to sacrifice body reserves, needing to forage regularly in regions of high productivity. Males thus appear capable of providing frequent meals for their chicks during the guard stage by foraging in local, less productive waters at the expense of their own body reserves. Demonstration that departure masses of birds prior to trips of long duration were lower than those prior to short trips supports the hypothesis that foraging decision in Adélie penguins is driven by a similar trade-off between the allocation of food to chicks and the storage of parental body reserves as has been described for other pelagic seabirds (Weimerskirch *et al.* 1997; Weimerskirch 1998).

Nest defence was identified as another factor likely to influence male and female foraging behaviours when chicks are small. Male Adélie penguins tend to defend their nests more vigorously against skua attack and human approach than do their mates during the time that the young are most vulnerable to predation and disturbance in the colony. Males also spend more time at the nest than their mates during the guard period. It is possible that sex differences in territorial behaviour contribute to the tendency for male birds to forage locally in preference to travelling further afield.

Variations in Adélie penguin diving behaviour between the sexes and as the chick rearing period progresses are also likely to be influenced by a variety of factors. Environmental conditions, particularly ice cover, change over the breeding season and can be related to variations in diving behaviour. Dive duration and mean percent bottom time are greater on long trips than on short, and penguins show a greater tendency to carry out short trips when fast ice is present than when there is open water. Once the ice disperses birds travel further to find food, and spend longer at their maximal depths. The greatest diurnal variation in dive frequencies was detected on short trips when fast ice was present. This is likely to be related to reduced light intensity from sea ice cover that prevents foraging during the hours when the sun is below the horizon. Surface ice formation at night when air temperatures are at their lowest may also prevent access by penguins to the water.

Variations in diving behaviour are likely to be directly related to prey distribution, especially during chick rearing when birds are foraging intensively to supply their growing offspring as well as themselves. Birds carrying out short trips tend to feed mostly on fish and amphipods, with benthopelagic fish species occurring in the diets of those birds making deeper trips and amphipods more common in stomachs of the shallowest-diving birds. Diving during the guard stage tends to be shallower than later in the season, and it is likely that prey items are being captured directly underneath the fast ice. During the crèche stage, when the ice is at its minimal extent, birds travel greater distances and dive longer and deeper. It is possible that as the sea ice disperses local food supplies become scarce, locally depleted or more sparsely distributed, and

breeding birds are forced to travel further from the colony to find sufficient food to support their growing chicks.

Variations in diving behaviour may also be related to sex differences in foraging behaviour and dietary preference. In Chapter 4 it was shown that during the guard stage female birds tend to make longer trips than males and feed predominantly on krill, while males carry out short trips and capture fish. The majority of short trips described in Chapter 5 were carried out by male birds feeding mainly on fish and amphipods, while the diving behaviour of female birds carrying out both long and short trips was associated with a diet consisting predominantly of *E. superba*. The increased proportion of bottom time shown by penguins carrying out long trips may be due to the fact that the birds travel to the edge of the continental shelf to feed particularly when they need to replenish their own body reserves, and are thus likely to be foraging most intensively at this time.

Successful rearing of chicks is principally dependent upon food availability over the breeding season. Reliable food supplies within a day's travel from the colony during the chick rearing period are vital to growth and survival of the offspring. Food availability during the guard stage appears to be most important, since chicks are most vulnerable to starvation when small and require frequent feeding to prevent stunted growth. A combination of adequate local food supplies in addition to reliable prey availability at the continental shelf edge appears to provide the best conditions for a high level of breeding success.

Inadequate prey availability (density and/or abundance) during chick rearing results in adult birds forsaking the needs of their chicks in preference to the maintenance of their own body condition, thus ensuring their own survival as first priority. Foraging trip durations increase as birds search more widely for food. Foraging range may also increase, as was the case in 1994-95 when the whole cohort of chicks died of starvation (Kerry *et al.* 1995b). Meal sizes will also diminish, thus enhancing the deleterious effects of infrequent feeding upon the dependent offspring. Chick growth rates will thus

decrease and, unless food supplies pick up dramatically, offspring may not attain sufficient body condition to survive at sea, even if they do manage to live long enough to fledge.

6.3 MONITORING PROGRAMMES

Studies undertaken as part of the Adélie penguin monitoring programme at Mawson have facilitated the understanding of a number of factors affecting breeding success. Biologists are now in a better position to determine the most useful parameters to monitor to provide further insights into the relationships between foraging behaviour, environmental conditions, prey distribution, krill stocks and breeding success. Variations in foraging behaviour and dietary preference between males and females and the relationship of these variations to the availabilities of both local and shelf-edge prey species have become apparent. Body condition of parent birds appears likely to be a driving force in the allocation of foraging effort between provisioning of chicks and self-maintenance. Foraging trip duration (particularly in combination with meal mass) has recently been identified as a sensitive indicator of colony productivity in terms of chick growth and survival (Irvine *et al.* in press).

Some recommendations regarding the parameters used for monitoring Adélie penguin populations with the aim of detecting changes in predator-prey relationships within the Antarctic marine ecosystem can thus be made. The CCAMLR Ecosystem Monitoring Program (CEMP) was set up in the late 1980's to monitor certain biological variables of selected species of krill predators with the objective of detecting changes in the marine ecosystem and attributing such changes to natural or man made (harvesting) causes. The studies described in this thesis have identified those parameters most sensitive to chick productivity at an intra-season level.

Duration of adult foraging trips during the guard stage is the parameter that appears to relate most directly to chick survival in a colony within a particular season. The guard

stage is when chicks are most susceptible to starvation and thus is when sufficient available food supplies are most important. It is important to know the sex of each bird monitored since male and female foraging behaviours differ. It is also important that foraging locations, diving behaviours and diet be studied concurrently to obtain a complete picture of what the penguins are eating, where they are obtaining their food and whether males and females are both able to forage effectively. Thus it can be recommended that dietary analyses be carried out in combination with satellite tracking and diving behaviour studies upon sexed birds whose foraging trip durations and body condition are known. Devices such as the APMS used in the Australian CEMP studies provide useful tools for collecting data to fulfil this latter requirement.

At this stage it appears that Adélie penguins in the Mawson region show their highest levels of breeding success in years when *E. superba* is present in the diet in large quantities (Chapter 4, unpublished data). However, we still have a very limited understanding of the factors that affect krill distribution and abundance in the water offshore from this region. Breeding success is often low in years in which the fast-ice persists longer than usual. The penguins seem to have trouble finding krill in such seasons, such as in 1994-95 when all the chicks starved to death. Why persistence of fast ice should affect the ability of the penguins to find food when they are foraging well north of the fast-ice region is unclear. However, it is possible that the same oceanographic process that affects the availability of krill in the Mawson region may also influence the timing of fast-ice breakout. Additional sea-based studies are required to fully understand the relationships between krill stocks and recruitment, winter and summer ice extent, and oceanographic changes. These studies will then need to be integrated with penguin monitoring programmes already in place to enable us to better comprehend the relationships between these predators and their prey.

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